Effects of a highly invasive plant (*Lantana camara*) on an agricultural flower visitation network

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Declaration

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General summary

Invasive alien plants threaten natural and agricultural pollination systems as they integrate into and disrupt flower visitation networks. Mango (*Mangifera indica*) production on commercial mango farms in Hoedspruit, South Africa, is an important part of the local economy. Mangoes require pollination for fruiting success, and depend on the native insect community, facilitated by managed bee colonies (*Apis mellifera*), to pollinate flowers. Managed honeybees and wild insect flower visitors to mango have previously been observed visiting other flowering plants in surrounding natural vegetation, including the alien invasive plant *Lantana camara*. *Lantana camara* and mango share similar floral characteristics and co-occur in close proximity, so they may share pollinators/flower visitors. Here, I determined *L. camara*'s influence on mango flower visitation networks, specifically whether it facilitates visitation, through greater abundance and diversity of insect flower visitors (facilitation), or competes for flower visitors (competition), and whether it supports mango flower visitors when mango trees are not in flower.

This study was conducted on the margins of three mango farms and bordering natural vegetation. Firstly, *L. camara*'s effect on mango flower visitation was investigated by comparing flower visitation to mango in plots with and without *L. camara* nearby. The presence of *L. camara* was associated with greater mango flower visitation, with increases in both flower visitor species abundance and richness. Secondly, the composition of flower visitor communities of mango orchard boundaries and bordering natural vegetation were evaluated. Although some flower visitors were shared between mango and naturally occurring plants, flower visitor community assemblages were significantly different between natural vegetation and mango orchard boundaries. In natural vegetation, flies, butterflies, wasps, wild bees and ants played a primary role in the visitation networks, whereas honeybees, wild bees and flies were the main visitors in mango orchards. The presence of *L. camara* significantly influenced community structure in both natural vegetation and orchards. Natural vegetation with *L. camara* had a more diverse flower visitor community than natural vegetation without *L. camara.*

Lantana camara seems to facilitate mango flower visitation during mango flowering, attracting a larger visitor abundance and species richness where it occurs in bordering natural vegetation and nearby mango orchard boundaries. However, *L. camara* was seen to be visited by few species known to visit mango outside of mango flowering, suggesting that *L. camara* may benefit more from facilitation than mango. Given its extreme invasive nature and threat to local plants which sustain native pollinators, *L. camara* should be removed from mango orchards and bordering natural vegetation. Furthermore, farm managers are encouraged to plant and maintain indigenous flowering plants, especially plants with a facilitative value to mango, in land surrounding mango orchards to sustain native wild pollinators beneficial to mango pollination.

Opsomming

Indringerplante bedreig natuurlike- en landboubestuiwingsisteme deur blombesoekingsnetwerke binne te dring en te ontwrig. Mango *(Mangifera indica)* produksie op kommersiële plase in Hoedspruit, Suid-Afrika, speel 'n belangrike rol in die plaaslike ekonomie. Suksesvolle mangovrugproduksie is afhanklik van bestuiwing deur inheemse insekte, gefasiliteer deur bestuurde heuningbykolonies *(Apis mellifera)*. Dit is vantevore waargeneem dat hierdie heuningbye en inheemse insekblombesoekers ook ander blomme besoek in die omliggende natuurlike plantegroei, veral *Lantana camara* wat in hierdie areas ook voorkom. *Lantana camara* en mango deel soortgelyke blomeienskappe en groei baie na aan mekaar op die buitenste rande van mango boorde. In hierdie studie bepaal ek *L. camara* se invloed op mangoblominsekbesoekers, en kyk spesifiek of dit mangoblombesoeking fasiliteer, deur om die aantal blombesoekers en blombesoekerspesies te verhoog (fasilitering), of mee kompeteer vir blombesoekers (kompetisie), en of dit mangoblombesoekers onderhou wanneer mango bome nie blom nie.

Hierdie studie is uitgevoer op die grensgebied tussen die mangoboorde en natuurlike plantegroei van drie mangoplase. Eerstens is *L. camara* se effek op mango ondersoek deur mangoblombesoeking te vergelyk tussen plotte met en sonder *L. camara*. Daar is gevind dat *L. camara* mangoblombesoeking fasiliteer deur om die aantal blombesoekers en besoekerspesies te verhoog. Tweedens is die gemeenskapsamestelling van blombesoekers in mangoboordrande en aangrensende plantegroei geëvalueer. Alhoewel sommige blombesoekers by mango én ander plante gevind word, is hul gemeenskapsamestelling aansienlik verskillend tussen die mangoboordrande en aangrensende plantegroei. Vlieë, skoenlappers, wespe, bye en miere speel 'n primêre rol in die blombesoekingsnetwerke van natuurlike plantegroei, waar hierdie rol in mangoboord-besoekingsnetwerke vervul word deur heuningbye, wilde bye en vlieë. Die teenwoordigheid van *L. camara* het die gemeenskapstruktuur in beide gebiede beduidend beïnvloed. Die aangrensende natuurlike plantegroei, waar *L. camara* voorkom, het ‘n meer diverse blombesoekersgemeenskap as dié sonder *L. camara*. Mangoboorde wat grens aan plantegroei, wat *L. camara* insluit, het soortgelyk 'n groter blombesoekerspesierykheid en aantal blombesoekers gehad.

Dit blyk dat, waar hierdie plant voorkom, *Lantana camara* mangoblombesoeking fasiliteer tydens mangoblomtyd sowel as om 'n groter aantal blombesoekersinsekte met ‘n groter spesierykheid te lok in beide die mangoboorde en aangrensende natuurlike plantegroei. Daar is egter geen bewyse gevind wat voorstel dat *L. camara* mangoblombesoekers ondersteun buite mangoblomtyd nie, wat aandui dat *L. camara* voordeel trek uit die fasiliterende verband met mango. Gegewe *L. camara* se uiterse indringende geaardheid en bedreiging aan die plaaslike inheemse plantgemeenskap wat inheemse bestuiwers onderhou, word *L. camara* se verwydering vanuit die aangrensende plantegroei aanbeveel. Dit word aanbeveel om *L. camara* se fasiliterende rol te vervang deur inheemse blomplante in dié areas aan te plant en natuurlike blomplantegroei te bewaar en te onderhou.

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Chapter 1. General Introduction

1.1 Alien Plant Invasion

Alien plant invasion is widely known to detrimentally affect natural and agricultural environments (Gurevitch & Padilla 2004; Mack *et al.* 2000; Pimentel *et al.* 2001). Of considerable concern are potential declines in diversity, abundance and interaction of beneficial arthropods, particularly pollinators (Allen-Wardel *et al.* 2008; Steffan-Dewenter *et al.* 2005). It is well established that invasive alien plants (IAPs) can easily integrate into native trophic networks (Carvalheiro *et al.* 2008; Lopezaraiza–Mikel *et al.* 2007) where they can shrink natural capital, compromise ecosystem stability and endanger economic productivity (Pejchar & Mooney 2009; Richardson & van Wilgen 2004).

The majority of IAPs share certain common traits that explain their invasional success and superior competitive ability. These are high growth and dispersal rates with IAPs often occurring in dense, impenetrable stands of vegetation, wide environmental and climatic tolerance enabling them to survive during adverse conditions and flourish vigorously during favourable conditions, and an ability to be highly adaptive to changing conditions, securing their survival in many diverse habitats (Kolar & Lodge 2001; Kühn *et al.* 2004; Pyšek & Richardson 2007). These traits enable the local abundance of IAPs to increase mostly at the expense of native plant communities (Daehler 2003; Vilà & Weiner 2004).

As our knowledge of introduced species has increased, so has our knowledge of the effects they have on ecosystems, including outcompeting local species (Human & Gordon 1997), interfering with mutualisms (Aizen *et al.* 2008; Bond & Slingsby 1984), increasing predation pressure (Kats & Ferrer 2003) and changing disturbance regimes (Brooks *et al.* 2004; Mack & D'Antonio 1998). Additional classic negative invasion impacts are disruptions in mutualistic networks of pollination and pollen dispersal (Schweiger *et al.* 2010; Traveset & Richardson 2006), reduction in native species richness and abundance, decreasing local species diversity (Sax & Gaines 2003), impacting on ecosystem services and human well-being (Pejchar & Mooney 2009) and changes in habitat and ecosystem functioning (Richardson *et al.* 2000; Vilà *et al.* 2006, 2009, 2010).

Conversely, IAPs may not always have negative impacts in the environments in which they occur (Schlaepfer *et al.* 2011). It is helpful to understand the environmental and invasional context and how the role of the IAP species traits interacts with these so that appropriate invasive status can be assigned (Pyšek *et al.* 2012). The overall performance of invasive alien and native plants depends on community-level processes and interactions. For example, alien plants that have longer flowering periods than their native counterparts tend to be more successful invaders (Küster *et al.* 2008).

1.2. Pollination: a vulnerable ecosystem service

Pollination illustrates one such vulnerable community-level process which is highly exploitable by IAPs (Bjerknes *et al.* 2007). Pollinators are sensitive to resource distribution and are attracted to areas of concentrated floral densities with high rewards (Potts *et al.* 2003). A significant invasional pattern is observed where IAPs attract native pollinators by producing showy floral displays, presenting additional food resources, decreasing native pollinator dependence on native plants (Bjerknes *et al.* 2007). Such increased availability of food resources allows for a larger flower visitor (native pollinator) community to be sustained in invaded areas (Heleno *et al.* 2008). This creates two irregularities; first, it decreases the pollination of native plants and, secondly, it increases the propagation of IAPs, accelerating their speed of invasion (Lopezaraiza-Mikel *et al.* 2007). If pollinators visit IAPs before visiting native plants, native plants' pollination and seed set are decreased through pollen limitation created by reduced flower visitation rates and interference with fertilization success by the deposition of heterospecific pollen (Bjerknes *et al.* 2007). Additionally, many alien plants have developed mutualisms with generalist dispersers and pollinators which facilitate their establishment and spread (Milton *et al.* 2007; Richardson *et al.* 2000). Invasive alien species may also form mutualisms with other invasive species, enhancing their probability of survival and increasing population size, a process known as "invasional meltdown" (Memmott & Waser 2002; Simberloff & von Holle 1999). These, and other more subtle, kinds of connections and interactions can be detected using ecological networks.

1.3. Ecological network analyses

Understanding natural ecosystems and ecological stability has been a difficult and frustrating task undertaken by natural scientists and ecologists. Due to the immense size of ecological systems and the complex relations found within, it is a daunting mission to unravel the intricate processes involved in understanding the common underlying natural laws. In dealing with this complexity, scientists have developed ecological network analyses to evaluate the multifaceted complex systems found within nature (Paine 1980).

Ecological network analyses tools can indicate the connectedness between species in any given habitat from which it is possible to discern web structure. These webs feature basic primary factors such as the number of species involved, number of connections per species, and the nature and intensity of interactions all obtained from direct observation in the laboratory or field. These factors enable webs to be visualised in a simple graphical format where certain measures of connectedness can be tested and evaluated equally. Improvements to analyses in network research increases the realistic interpretations of ecological networks, broadening our understanding of community stability, natural ecological processes and relationships. Network research can be applied to both pure and applied ecological questions.

Thus far, applied research has provided insight on the conservation of rare plants, impact of habitat management, biocontrol effectivity, assessment of ecological restoration activities, ecosystem services and the effects of invasive alien species on network dynamics, to mention but a few (Carvalheiro *et al.* 2008; Memmott 1999; van Veen *et al.* 2006). For this purpose, ecological network research provides valuable assessment capabilities, especially considering research done within economically important zones such as agricultural farmland. Information on these subjects is generally gathered from analysis of consumer-resource webs constructed from known/observed relationships between species. Such consumer-resource relations are studied through different types of webs, such as predator-prey, host-parasitoid, and plant-pollinator (including flower visitation) networks.

1.4. Plant-pollinator networks

Pollination is a key ecosystem function that presents an economic and agriculturally significant consumer-resource network (Kremen 2005). It is estimated that 35% of global crop production, and 60% - 80% of wild plants worldwide, depends upon animal pollination (Klein *et al.* 2007). Given the importance of this valuable ecosystem service, it is imperative that ecological studies focus on identifying emerging problems within plant-pollinator networks. Such studies have identified and recognised the recent colony collapse disorder in European honeybee colonies in Northern America and Europe starting in 2006, and although the cause hasn't clearly been identified, it has been attributed to an increase in pathogen exposure and other biotic stress factors (Johnson 2010; van Engelsdorp *et al.* 2009). Other plant-pollinator network studies are now also showing potential for predicting pollinator behaviour in light of species loss, invasion success, and their vulnerability to variable land-use impacts (Kaiser-Bunbury *et al.* 2010; Romanuk *et al.* 2009; Weiner *et al.* 2014). Practical applications of network studies provide useful conservation tools for assessing environmental conditions. Gibson *et al.* (2006) assigned values to flower visitors in terms of pollinator importance through the construction of visitation and pollen transport networks, which assisted in the appraisal of pollination services within restored heathlands. Flower visitation networks enable visualisation of the relationship between plant and invertebrate species within a system, and how these interactions can influence flower visitation of both wild and crop plants, which make them a useful tool in understanding alien plant invasional patterns within agricultural networks (Memmott 2009).

1.5. Invasive Alien Plants and Plant-Pollinator networks

As one of the best-studied ecosystem services, pollination and flower-visitor networks provide understanding of the qualitative and quantitative links between providers and beneficiaries within an ecosystem. They also allow expansive research on the invasive effects of alien plants and how they may affect pollinating insects. IAPs have been observed to exert negative (competitive), positive (facilitative, mutualistic) and neutral effects on flower visitation and pollination networks within natural

habitats (Bjerknes *et al.* 2007). For example, experimental studies show the competitive effects of invasive alien species *Lythrum salicaria* (purple loosestrife) within close proximity to the native plant *L. alatum* (winged loosestrife) through reduced flower visitation rates and reproductive success (Brown *et al.* 2002), although other studies found that this same plant facilitated pollination of native species (Lopezaraiza-Mikel *et al.* 2007). Similarly, *Impatiens glandulifera* has been found to lure pollinators from native flora, which consequently led to reduced seed set and general fitness of native plants (Chittka & Schurkens 2001). Other observational studies report decreased flower visitation rates in natural flora where IAPs occur and higher visitation rates for IAPs in prairie and island plant communities (Larson *et al.* 2006; Moragues & Traveset 2005).

In another study, two IAPs, *Carpobrotus* and *Opuntia* sp., played a central role in Mediterranean ecosystems, with higher levels of insect interaction compared to that of the native flora (Bartomeus *et al.* 2008). Different effects were found for each IAP, however: *Carpobrotus* provided a positive influence by facilitating pollinator visits to natural flowering plants, whereas *Opuntia* negatively influenced native flora, by competing with natural plants for pollinators (Bartomeus *et al.* 2008). In a comprehensive study on the integration of five IAPs (i.e. *Carpobrotus sp*., *Impatiens glandulifera*, *Opuntia sp*., *Rhododendron sp*. and *Solanum sp*.) into natural plant-pollinator networks across Europe, Vilà *et al.* (2009) found that the individual presence of these invasive plants either had a positive, neutral or negative effect on pollinator visitation of certain native species. The effect of IAPs on the local community can be density-dependent, however. In the Andes, Muñoz & Cavieres (2008) found the IAP *Taraxacum officinale* reduced seed output and disrupt pollination services to neighbouring native plants only when occurring in high densities. In low densities, *T. officinale* actually worked to attract native pollinators to isolated areas, where native plants benefited from their presence by sharing pollinators. Contrariwise, Nielsen *et al.* (2008) found no significant effects of flower visitation to *Mimulus guttatus* in close proximity to invader species *Heracleum mantegazzianum*. Overall, negative effects on native plant-pollinator interactions seem to dominate, particularly when flower colour and flower symmetry are similar between IAP and native plant species (Morales & Traveset 2009).

1.6. Flower Visitation Networks in Agricultural Environments

The growing base of pollination network literature addresses plant-pollinator networks in natural habitats, although as much, if not more, understanding is needed of pollinator networks in agricultural environments. Valuable insight on crop pollination has been attained by studies on pollination networks within sunflower fields and mango orchards, where it has been found that the promotion of flowering plants and preservation of natural floral patches contribute greatly to crop yield (Carvalheiro *et al.* 2011, 2012). Increased floral abundance within natural vegetation in close proximity to farmland has beneficial effects on crop pollination (Carvalheiro *et al.* 2010; Chacoff & Aizen 2006). Crop pollination

services are improved through the spill-over effect of pollinators from natural habitat to nearby agricultural land (Blitzer *et al.* 2012; Garibaldi *et al.* 2011). Contrariwise, in certain circumstances, flowering crops may support native pollinators as seen in improved bumble bee abundance in Afrotropical forest remnants scattered throughout farmland in Western Kenya (Hagen & Kraemer 2010). The greater resource availability provided by mass flowering crops, such as mango, create a "magnet effect" to native/generalist pollinators which may result in increased flower visitation to co-flowering plants in the vicinity (Feldman *et al.* 2004; Hanley *et al.* 2011; Holzschuh *et al.* 2013; Westphal *et al.* 2003).

Whilst working on pollination services in mango (*Mangifera indica*) in the Limpopo Province, Carvalheiro *et al.* (2010) found that several alien species (e.g., *Lantana camara*, *Melia azedarach*, and *Bidens pilosa*) are becoming integrated into the native ecological networks through shared flower visitors. This could imply that pollinators of crops might be using the resources provided by exotic plant species, and so alien presence may change pollinator visitation to crop flowers. To the best of the author's knowledge, this is the first study to examine the effect of alien plant invasion into agricultural flower visitation networks, as most studies have focussed on the effects of invasion in natural environments.

The South African agricultural economy is largely supported by soft fruit produce, which holds great economic importance locally and internationally (SSA 2013). Due to the growing body of evidence that the negative impacts of habitat invasion affects pollinator assemblages, which could in turn affect crop pollination, it is important to understand the processes by which IAPs infiltrate these agricultural systems. Understanding the degree to which agriculture could be endangered by competition for pollinators or, in contrast, benefited through facilitation services is useful to the efficient management of crops.

*1.7. Mango (*Mangifera indica*)*

The subtropical fruit mango, *Mangifera indica*, originates from the Malay area in South East Asia and is cultivated commercially in areas with sub-tropical climates, including South Africa (Mukherjee 1997; Waite 2002). Mango flowers are pollinated by an array of flower visiting insects, where the most general pollinators tend to vary amongst areas. Generally, flies (Calliphoridae and Syrphidae) are the most frequent flower visitors in Costa Rica and India, whereas wasps and native bees (*Trigona* sp.) visit mango flowers more frequently in Australia, Israel and South Africa (Anderson *et al.* 1982; Dag & Gazit 1996; Eardley & Mansell 1994; Singh 1997). The native bee species *Apis cerana* is a common mango pollinator in Thailand (Wongsiri & Chen 1995). The efficient mango pollinating contribution of flies and ants have also been recognised in Australia, Kenya, Jamaica and South Africa (Anderson *et al.* 1982; Carvalheiro et al. 2010; Free & Williams 1976).

1.8. Lantana camara

Lantana camara (L.), native to Central and South America, is a particularly aggressive and troublesome invasive plant species within natural and agricultural environments worldwide (IUCN 2001; Sharma *et al.* 2005; Vardien *et al.* 2012). The species is a woody perennial shrub with weedy characteristics (i.e., fast growing and competitive). It has spiny branches and stems, and inflorescences of small whitish to pink flowers (Mathur & Mohan Ram 1986). The species has a wide climatic tolerance, which has enabled it to become naturalized within Australia, Africa (including South Africa) and India (Sharma *et al.* 2005; Vardien *et al.* 2012). Its impact on agriculture, forestry and native biodiversity is marked because of the species' invasive characteristics, such as rapid vegetative growth, aggressive competitive ability, fire tolerance, high seed production, allelopathy, high percentage fruit set (85%) and proliferation throughout the year in ideal environmental conditions (Ghisalberti 2000; Gooden *et al.* 2009; Sharma *et al.* 2005).

Along with its ecological impacts, *Lantana camara* (hereafter referred to as *Lantana*) could also infiltrate natural and agricultural pollination systems, as a large diversity of pollinators have been found to pollinate *Lantana* within natural environments (Dronamraju 1960; Goulson & Derwent 2004; Hamm 2012; Mather & Mohan Ram 1978; Sharma *et al.* 2005). Sharma *et al.* (2005) review *Lantana*'s dependence on pollinators, such as thrips, honeybees (*Apis mellifera* L.), hummingbirds (*Amazilia* sp.) and butterflies, for improved pollination success and seed set, although evidence has been found of its successful capability for autonomous self-pollination (Barros *et al.* 2001; Hamm 2012; Rambuda & Johnson 2004). *Lantana*'s primary pollinators vary greatly between different areas. Goulson & Derwent (2004) found honeybees (*Apis mellifera*) to be the primary pollinators for *Lantana* in natural areas along eastern Australia. Reports from India indicate thrips (Thripidae, Phlaeothripiae) (Mather & Mohan Ram 1978) and butterflies (Hesperiidae, Nymphalidae, Papilionidae, and Pieridae) as pollinators (Dronamraju 1960). Hummingbirds and Lepidoptera (Nymphalinae and Satyrinae) were recorded as possible pollinators within *Lantana*'s native range in Costa Rica (Hamm 2012).

1.9. This Study

To date, studies of the impact of *Lantana* on pollination networks have focussed primarily on its effects on pollination systems within natural environments (Goulson & Derwent 2004; Hamm 2012; Schemske 1976; Vardien *et al.* 2012) yet there is no quantitative evidence of its effect on insect-flower interactions within agricultural systems. Given that *Lantana* flowers throughout the year, it has the potential to become integrated into the pollination networks of many crop species as an additional food resource for insect flower visitors.

This study aims to understand the role IAPs could have in agricultural and ecological food webs. This is essential to evaluate the needs of targeted management practices that may benefit farmers and contribute to the conservation of natural plant and animal communities within the adjacent natural habitats. In addition, understanding how alien organisms become integrated into networks can aid risk assessment, as we increase our understanding of the full suite of effects they may have on indigenous biodiversity patterns and processes. Creating flower visitation networks for this production system will also provide a deeper understanding on the effects invasive alien plants have on pollination networks within agricultural systems.

Limpopo, an agriculturally-productive province within South Africa, is at risk of severe infestation by invasive alien plants (including *Lantana*) if not properly managed (Baars 1999, 2002; Vardien *et al.* 2012). Farmers in South Africa are legally obliged to remove *Lantana*, as a Category 1 invasive plant within the Conservation of Agricultural Resources Act, 1983 (Act No 43 of 1983) (CARA), from their agricultural estates. IAP infestation occurs mostly in semi- and fully disturbed areas (due to the weakened state of the natural vegetation competitive ability), especially those surrounding agricultural lands. For this reason, thick alien stands are commonly found around orchards such as in our study area. The Agricultural Research Centre suggests that efficient and cost-effective management of *Lantana* involves a combination of biological, mechanical and chemical control methods. Biological control of *Lantana* may decrease the rate of reproduction and growth, and mechanical and chemical controls limit its vegetative growth from developing into extremely dense thickets (ARC 2010; Vardien *et al.* 2012).

Mango flowers are largely self-incompatible, resulting in poor seed (and fruit) set from self-pollination, and therefore require the services of visiting insect pollinators to assist in cross-pollination between flowers (Anderson *et al.* 1982). Thus it is useful to understand the factors influencing pollinator assemblages within mango orchards (Burd 1994; Free 1970).

Bjerknes *et al.* (2007) has listed floral attractiveness, flower morphology, population size and density, generalization/specialization and pollinator dependence as plant characteristics which make pollination networks susceptible to disturbance effects by invasive alien plants. Both *Lantana* and mango flowers are nectar producers, occur in inflorescences with small whitish to pink flowers (<20 mm) and according to the literature (Carvalheiro *et al.* 2010; Goulson & Derwent 2004) share honeybees as flower visitors. Based on this information, both plants' flowers share enough defining qualities which may cause pollinators to alternate between them if they should co-occur in the same area, creating a disruption in the natural pollination network occurring within and surrounding these mango plantations.

In Chapter 2, I assess whether *L. camara* has infiltrated the flower visitation network of mango orchards in South Africa. This involves determining whether *Lantana* provides possible competitive or facilitative influences on mango flower pollination by affecting the flower insect-visiting frequency. By

evaluating flower visitation (species richness and abundance) to mango on orchard boundaries in close proximity to natural veld (with *Lantana* present/absent), *Lantana*'s influence on this flower visitation network can be established. I specifically look at the question as to whether *Lantana camara* affects mango flower insect visitation by providing facilitation (increased flower visitation by insects) or competition (decreased flower visitation by insects). Additionally, *Lantana*'s support of mango flower visitors (pollinators) outside of the mango flowering season is investigated.

In Chapter 3, I compare and evaluate the insect-flower visitor community assemblages between flower visitor networks on the fringes of mango orchards in South Africa. Specifically, I investigate how insect flower visitor community composition differs between mango orchard boundaries and bordering natural vegetation, with and without *Lantana*. This information allows comparison of insect assemblages between areas, determining community structure, as well as which insects are shared as pollinators between mango and *Lantana* (indicating which insects tend to be more generalists visitors). A community-level approach is used, whereby insect species richness, abundance and species richness estimators of the plant-visitor community are investigated within study plots. While writing this thesis, I have written Chapters 2 and 3 as papers to be published by scientific journals, and as such, replication of information is regrettably unavoidable.

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Chapter 2. How does *Lantana camara* affect mango (*Mangifera indica)* flower insect visitation?

ABSTRACT

Exotic plant species integrate into native trophic networks, with invasive plants often disrupting native pollination systems. In Hoedspruit, South Africa, the invasive alien plant *Lantana camara* occurs in dense stands bordering agricultural crop mango. Similar flowering times and floral characteristics between these two plants raises the question as to whether they share flower visitors and how *Lantana* influences flower visitation of mango. Insect flower visitation surveys were conducted in mango orchard margins and bordering natural vegetation, with and without *Lantana* present, before, during and after mango flowering. Mango flower visitor species abundance and richness were assessed and compared between plots where *Lantana* was present and absent. Additionally, flower visitation of *L. camara* occurring in natural vegetation was investigated to determine whether it supported mango flower visitors before and after mango flowering. Constructed flower visitation networks and generalized linear mixed models show a positive correlation between *Lantana* presence with mango flower visitor's abundance and species richness. Higher mango visitation rates were seen for Diptera (syrphids) and Hymenoptera (honeybees and ants) where *Lantana* was present than where it was absent. Few mango flower visitors were seen visiting *L. camara* outside of mango flowering times. This case study shows that *Lantana camara*'s presence facilitates increased flower visitation of nearby mango, potentially leading to increased fruit production. As *Lantana* is an aggressive alien plant, management recommendations are made to remove *Lantana* and replace with native flowering plants capable of providing a similar facilitative use, to aid in crop pollination.

2.1. INTRODUCTION

It is well established that exotic plant species can integrate into native trophic networks (Carvalheiro *et al.* 2008; Lopezaraiza–Mikel *et al.* 2007); and if they become invasive (Invasive Alien Plants, IAPs), they can shrink natural capital, compromise ecosystem stability and endanger economic productivity (Pejchar & Mooney 2009; Richardson & van Wilgen 2004). As our knowledge of introduced species has increased, so we have come to realise the effect they have on ecosystems, specifically outcompeting local species (Human & Gordon 1997), interfering with mutualisms (Bond & Slingsby 1984), increasing predation pressure (Kats & Ferrer 2003) and changing disturbance regimes (Brooks *et al.* 2004; Mack & D'Antonio 1998). When invasive species infiltrate ecological networks, their presence can have negative (competition) or positive (facilitation) implications for native insect populations influencing pollination success of natural flora (Lopezaraiza-Mikel *et al.* 2007; Memmott & Waser 2002).

Bjerknes *et al.* (2007) reviewed the competitive effects of invasive alien species and found they reduced flower visitation rates and reproductive success in natural flora within close proximity to invasive alien plants (see Brown *et al.* 2002; Chittka & Schurkens 2001). This was supported by observational studies

reporting decreased flower visitation rates to natural flora and higher visitation rates for invasive alien plants, compared to the flower visitation to native plants (Larson *et al.* 2006; Moragues & Traveset 2005). A meta-analysis of the effects invasive alien plants (IAPs) have on native plants' pollinator visitation and reproductive success found dominant negative impacts to be decreased visitation rates, pollination success and seed-set of native flora, which became more marked with increasing IAP abundance and shared floral characteristics (Morales & Traveset 2009). The effects of IAPs infiltrating ecological webs are not always negative, however. Nielsen *et al.* (2008) found no significant effects on flower visitation to *Mimulus guttatus* as a result of being in close proximity to invasive *Heracleum mantegazzianum*. In another study, two IAPs, *Carpobrotus* and *Opuntia* sp., played a central role in Mediterranean ecosystems, with higher levels of insect interaction compared to that of the native flora (Bartomeus *et al.* 2008). The two IAPs differed in their effects on the system, however. *Carpobrotus* provided a positive influence by facilitating pollinator visits to natural flowering plants, whereas *Opuntia* negatively influenced native flora, competing with natural plants for pollinators (Bartomeus *et al.* 2008). Vilà *et al.* (2009), in a study on the integration of five alien plant species (i.e. *Carpobrotus* sp., *Impatiens glandulifera*, *Opuntia* sp., *Rhododendron* sp. and *Solanum* sp.) into natural flower-insect interaction networks across Europe, found that the individual presence of these invasive plants had varying effects (positive, neutral or negative) on pollinator visitation of certain native species.

Successful pollination of animal-pollinated crops, which represent 35% of the world's crops, is required to meet society's increasing demands of these foods (Aizen *et al.* 2009). This necessitates a broad understanding of the factors that influence pollinator assemblages within agricultural systems (Burd 1994; Free 1970). Given the various possibilities in IAP interactive effects on native insect populations within natural environments, and the importance of pollinator-dependent crops in human diets, it is important to understand similar competitive or facilitative effects that invasive plants may have on pollinator-dependent crops.

It has been established that Limpopo, an agriculturally productive province within South Africa, is at risk of severe infestation by invasive alien plants (such as *Lantana camara*) if proper management operations are not in place (ARC 2013; Vardien *et al.* 2012). Of particular concern is the integration of IAPs into natural vegetation surrounding farmlands, as seen near commercial mango farms in the Hoedspruit area (Carvalheiro *et al.* 2010). These IAPs, which tend to occur in disturbed habitat around agricultural land, pose a risk to ecosystem services essential to agriculture, e.g., pollination (Cook *et al.* 2007). IAPs could integrate into pollination networks of infested agricultural land, luring pollinating insects away from crops and displacing pollinating insects further away from crop plants (Carvalheiro *et al.* 2012). This is of considerable importance to mango as mango flowers have poor seed set from self-pollination and, therefore, rely heavily on visiting insect pollinators (Anderson *et al.* 1982). Indeed, these risks could be exacerbated by the seasonal addition of managed honeybee hives (*Apis mellifera*)

during mango flowering intended to aid crop pollination, as increased pollinator abundance could lead to higher flower visitation of alien plant species nearby mango and so IAP reproductive success is increased leading to their successful proliferation (Hanley *et al.* 2011).

Whilst working on pollination services in mango (*Mangifera indica*) in Limpopo, Carvalheiro *et al.* (2010) found that several alien plant species (e.g., *Lantana camara*, *Melia azedarach*, and *Bidens pilosa*) to be well-integrated into the native ecological network. This could imply that pollinators of crops might be using the resources provided by exotic plant species, and so the presence of alien species may change flower visitation to crop flowers. *Lantana* flowers throughout the year, and often abundantly, so its flowers present possible food resources to native pollinating insect populations during mango flowering, as well as during the pre-mango-flowering stage (December – June) when little else is flowering (*pers. obs.*).

Mango (*Mangifera indica*) and the invasive alien *Lantana camara* (hereafter referred to as *Lantana*) share floral characteristics by having similar floral attractiveness, morphology, population size and density, as well as both being dependent on generalist and specialist pollinators (Anderson & Dobson 2003; Anderson *et al.* 1982; Barros *et al.* 2001; Carvalheiro *et al.* 2010; Hamm 2012; Schemske 1976; Sharma *et al.* 2005; Waite 2002). These shared characteristics increase the possibility of interactive effects between them (Bjerknes *et al.* 2007). *Lantana* is known to have adverse effects on natural ecosystems and native plant species diversity, and is an aggressive weed that has predominately invaded South Africa's eastern provinces of KwaZulu-Natal, Limpopo and Mpumalanga (Vardien *et al.* 2012). It often forms large stands in environmentally disturbed areas, particularly in the boundaries of agricultural land and nearby natural vegetation (ARC 2010). These invasive traits are attributed to its allelopathic effects on native plants and its ability to outcompete natural flora for resources (Sharma *et al.* 2005).

Where *Lantana* and mango coexist, they could compete with or facilitate each other for pollination services, as both plants' flowers produce nectar, occur in inflorescences with small whitish to pink flowers (which are very similar in size, <20 mm) and have been found to share honeybees as flower visitors (Carvalheiro *et al.* 2010; Goulson & Derwent 2004). The following questions were asked as to the effect of *Lantana* on mango flower visitation: (1) Does *Lantana camara* compete with or facilitate mango flower visitation?, and (2) does *L. camara* serve as additional floral resource to mango flower visitors before and after mango flowering? To determine this, I compare mango flower visitor species richness and abundance in the presence and absence of *Lantana*, as well as evaluate the flower visitors of *Lantana* before and after mango flowering. Given *Lantana's* attractive floral attributes, and shared flower visitors with mango during mango flowering, I expect competition for flower visitors with mango and anticipate that *Lantana* supports mango flower visitors out of mango flowering season, as

Lantana flowers year-round. If *Lantana* does increase pollinator diversity and/or abundance to mango flowers, thus increasing mango fruit yield, and supports mango flower visitors outside the mango flowering period, then *L. camara* (or a similar native plant) would be desirable to farmers. Alternately, if they have little or no pollination value, then their removal would be encouraged as *Lantana* is known to be a highly invasive plant presenting potential damage to the natural functioning of this ecosystem.

2.2. METHODS

2.2.1. Study area and design

Surveys were conducted on commercial mango farms near Hoedspruit, Limpopo Province, South Africa, within the Kruger to Canyons Biosphere Reserve (Figure 2.1). The vegetation in the area is classified as Granite Lowveld, characterised by large *Acacia (Vachellia) nigrescens, Ficus stuhlmannii* and *Sclerocarya birrea* trees, with various *Combretum* and *Dichrostachys* shrub species and *Digitaria* and *Eragrostis* grasses (Mucina & Rutherford 2006). Observational plots were located on three commercial farms subject to similar management practices (i.e., pesticide application of neonicotinoids or organophosphates, cropping system, irrigation, non-specific naturally occurring plant clearing and harvesting period), as well as similar abiotic conditions (climate, soil and sunlight exposure). Soil water and nutrient content, important variables in crop production, are monitored throughout the year to keep conditions optimal for mango production (J. du Preez and G. Schoeman *pers. comm.*), presenting minimal variation in abiotic conditions. Mango orchard sections (standard size = 165 x 55 m) are divided by windbreaks, planted with *Casuarina* sp. (beefwood). These plantations are bordered by natural vegetation with varying levels of infestation by invasive alien plants such as *Lantana*.

I carried out monthly flower visitation surveys in fixed observational plots across each of the three farms (Bavaria, Jonkmanspruit and Mohlatsi) from June to October 2013. Forty fixed plots, partitioned into 20 paired plots, were located on each farm. Paired plots consisted of one plot on the edge of the mango orchard and another in nearby bordering natural vegetation (ca. 15 m from one another), 10 of these plots in mango and natural margin had *Lantana* present and the other 10 in mango and natural margin were without *Lantana* (Figure 2.2). The paired plots were widely dispersed (100 m to >300 m from one another) over the farms to include up to five mango cultivars (i.e. Kent, Keitt, Sensation, Tommy Atkinson and Shelly), and were all at least 150 m away from large water bodies.

Plots were chosen to represent varying degrees of influence that *Lantana* may have on mango flower visitation; (i) a range of flowering densities of *Lantana* and other naturally occurring flowering plants (low, medium, high), (ii) mango flowers on orchard margins in varying proximity to natural vegetation, containing *Lantana* stands and other naturally occurring plants (between 2 and 17 m) and (iii) mango flowers on orchard margins near natural vegetation boundary with no *Lantana* present. All sites had

managed honeybee (*Apis mellifera scutellata* Lepeletier) colonies during the mango flowering season (i.e., July to September), roughly about one colony per hectare.

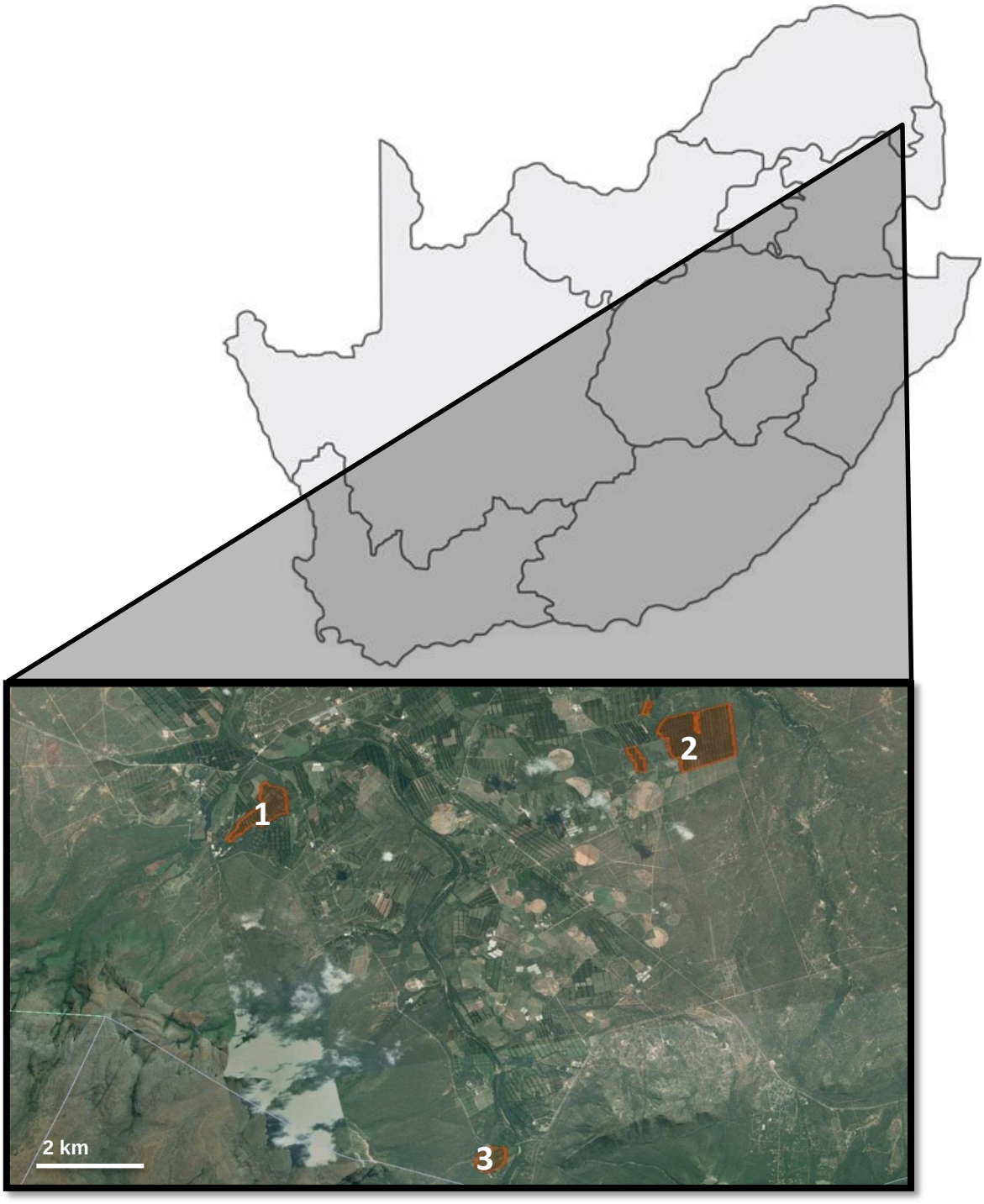

Figure 2.1. Map of South Africa (top) and the three mango farms, Jonkmanspruit (1), Bavaria (2) and Mohlatsi (3), coloured in orange (bottom) near Hoedspruit, Limpopo (Google Inc. 2014).

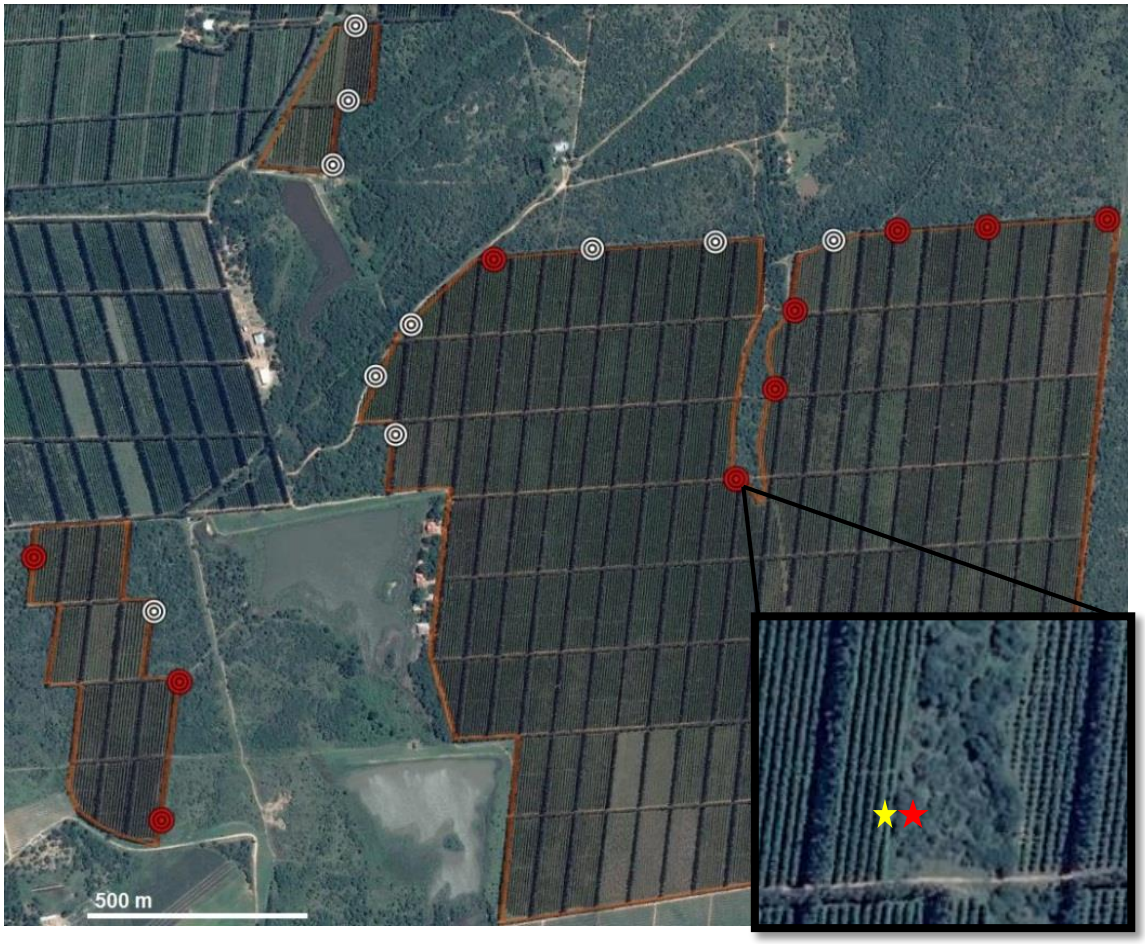

Figure 2.2. Image of the paired observational plots on Bavaria Fruit Estate, where mango plots border natural vegetation with *Lantana* (white circles) and without *Lantana* (red circles). One such paired plot is depicted (bottom right) where the mango orchard border (yellow star) is near natural vegetation margin (red star) (Google Inc. 2014).

2.2.2. Flower visitation surveys

Flower visitation surveys were conducted before (June), during (July to September) and after mango flowering (October). These surveys were carried out by two observers. Observers stood at one point for 20 minutes to detect any flower-insect interactions in a plot 2 m ahead and 2 m across of them (i.e., 1 m to either side of the observer). Flower-insect interaction or 'flower visitation' is defined as the movement of a potential pollinator on or in the flower tube where it is possible that the insect has come into physical contact with flower stamens, which may potentially lead to pollen transfer. Each insect visiting one flower was recorded as an individual flower visitation event, and subsequent flower visitation to other flowers by the same individual in the observation plot was counted and recorded (e.g. flower visitation by one insect: one visit to three flowers = three interaction observations, three visits to one flower = one interaction observation).

As mango anthesis is diurnal, visitation surveys were done between 08h00 and 16h00 on warm dry days (20-39 °C) with slow wind speed (0-4 km h^{-1}). At each plot, timed observations were done (20 min per plot) where all insect-flower interactions were recorded, with an individual of each insect and plant species being sampled for identification purposes (done under the Limpopo Provincial Government Permit No. 001-CPM401-00005, issued on 14/06/2013). In natural margin plots, floral density (individual flowers per unit area) was determined by counting the total number of open flowers. Where *Lantana camara* was treated as the focal species, other flowering plants present was considered as part of an assemblage of naturally occurring flowering plants. Naturally occurring flowering plants (NOFPs) are considered to be any flowering plants (native or exotic sp.) present in the observational plots other than *L. camara* and mango. Mango flower densities were estimated by averaging the total number of flowers counted on three random inflorescences and multiplying it by the amount of inflorescences found within the perimeter of the observational mango plot.

Flower visitation surveys in the natural vegetation during June and October (i.e., before and after mango flowering) included the focal species, *Lantana camara*, Daisy sp., *Jasminum multipartitum* (wild jasmine), *Justicia flava*, as well as other non-indigenous flowering plants (also considered to be naturally occurring flowering plants, NOFPs) such as *Bidens pilosa* (Blackjack), *Tridax procumbens*, *Melia azedarach* (Syringa), *Onopordum acanthium* (Scotch thistle), and *Ipomoea purpurea* (common morning glory). Fewer plants were flowering during winter (July to October) in the natural vegetation with the floral community being dominated by *Lantana camara*, *Ipomoea purpurea* and *Tridax procumbens*. Managed honeybee colonies (*Apis mellifera scutellata*) were placed at densities of approximately one hive per hectare within orchards during the mango flowering period.

2.2.3. Ecological networks, statistical analyses, and modelling

Visitation data (species interaction per flower) from all 60 mango plots for all months were pooled to visualize flower-insect visitor webs, using software (Bipartite package) written in *R* (Dormann *et al.* 2009). Data were pooled to display all insect-plant interactions observed for flower visitors on mango in orchard margins in the presence and absence of *Lantana* in neighbouring natural vegetation as well as for *Lantana* flower visitation before, during and after mango flowering, to discern changes in flower visitor species abundance and proportion of overall flower visitation. Here, abundance of species equates to the number of interactions (number of visits to different flowers) by that species. Information regarding the status of flower visitors as mango and *Lantana* pollinators has been determined from published literature and field guides (Barros *et al.* 2001; Barrows 1976; Chin *et al.* 2010; Goulson & Derwent 2004; Hamm 2012; Louw & Labuschagne 2011; Muthoka & Mananze 2005; Sharma *et al.* 2005; Waite 2002).

Overall flower visitor abundance and species richness were compared between mango plots in the presence and absence of *Lantana* using paired t-tests. Data were not normally distributed and was therefore log transformed for analyses. Correlations between mango flower visitor abundance and species richness with *Lantana* and NOFP floral density, and mango floral density, were assessed using Spearman's rank correlation coefficient. Both statistical tests' parameters and assumptions were checked and satisfied during analyses.

Generalized linear mixed models (GLMMs) with Poisson distribution (log-link function and chi-squared tests) were used to assess how overall mango flower visitation (species abundance and richness) was affected by *Lantana*. Backward elimination of predictor variables tested all possible combinations for the best-fit model, dropping non-significant factors at each stage. The fixed effects were floral abundances of mango, *Lantana*, and NOFPs (including the interactive effect of *Lantana* and NOFPs) and distance between paired plots, and the random effects were month, plots within farms and cultivar. The best-fit model with the lowest corrected Akaike Information Criterion was used as selection criterion as a second order AIC which is corrected for small sample sizes (AICc), providing greater penalty for extra parameters (Burnham & Anderson 2002). GLMMs were constructed and analysed in *R* using packages lme4 and MuMIn (Bates *et al.* 2014; Burnham & Anderson 2002; R Development Core Team 2014). Variance explained, R^2 (conditional and marginal), were calculated to determine 'goodness of fit' of the best-fit model in R with packages lme4 (Bates *et al.* 2014; Nakagawa & Schielzeth 2013). All statistical analyses, ecological networking and modelling were performed with the software *R* (R Development Core Team 2014).

To determine similarities between the flower visitor assemblages (in terms of abundance) in natural vegetation before, during and after mango flowering, permutational multivariate analyses of variance (PERMANOVA) was computed in PRIMER 6 (PRIMER E 2009). Bray-Curtis measures assessed similarities between species data, which had been square-root transformed to increase weight of rare species (Anderson 2001). F- and *P*-values obtained from pairwise tests, all analyses with 9999 permutations, were compared to assess differences between sampling events. Post-hoc analysis of sampling times in natural vegetation were done using canonical analysis of principal coordinates (CAP), whereby particular gradients of interest in a multivariate dataset may be outlined in plot form (Anderson 2008; Anderson & Willis 2003). The data used for analyses on *Lantana camara*'s flower visitor insect assemblage is obtained from three surveys split into three groups ('before', 'after' and 'during' mango flowering). Time restrictions on data collections allowed for only one survey to represent the 'before' and 'after' groups. Therefore where group data was used for comparison, the 'during' group data was represented by the survey done in August (peak mango flowering time).

2.3. RESULTS

2.3.1. Does Lantana *compete with or facilitate mango flower visitation?*

A total of 1468 insect-mango interactions were observed throughout all mango plots, with a total floral density of approximately 1 325 000 flowers, over the entire mango flowering season. Of the 1468 insect-mango interactions observed, the vast majority (1003) were in plots neighbouring natural vegetation containing *Lantana*, indicating higher insect visitation rates for mango plots neighbouring *Lantana* (abundance: t-test, $t = 8.11$, Df = 29, $P < 0.001$; species richness: t-test, $t = 5.19$, Df = 29, $P < 0.001$) than that of mango neighbouring natural vegetation without *Lantana* (465 interactions; Figure 2.3). Forty seven of the 76 mango flower visitor species present in mango orchards were seen foraging on other naturally occurring flowering plants in neighbouring natural vegetation. Forty three of these 47 species specifically visited *Lantana camara*, most notably, species belonging to the Dipteran (flies) and Hymenopteran (Formicidae, Apidae and Anthophoridae) groups (Figure 2.3).

The greatest increase in total mango flower visitor abundance were seen for Diptera (Muscidae sp., Syrphidea groups *Ischiodin* sp., *Eumerus* sp. and *Eupeodes* sp.) [118% increase], honeybee (*Apis mellifera*) [144% increase] and thrips (Thysanoptera) [101% increase] between mango plots where *Lantana* was present and absent (Table 2.1).

Table 2.1. The effect of *Lantana camara* on mango flower interactions (int.), of different insect flower visitor groups, in mango orchard boundary plots with and without *Lantana* nearby.

Insect Group	Int. on mango flowers with *Lantana* absent	Int. on mango flowers with *Lantana* present	Effect of *Lantana*
Ants	30	28	-2
Butterflies	5	29	+24
Native bees and wasps	7	15	+8
Flies	180	393	+213 (118% increase)
Honeybees	149	365	+216 (144% increase)
Thrips	53	107	+54 (101% increase)

Total species richness was also greater in mango plots with *Lantana* (64 species) than mango plots without *Lantana* (33 species). In plots where *Lantana* was present, 28 insect species (not observed in mango plots where *Lantana* was absent) had fewer than 5 interactions with mango flowers over the entire sampling period, indicating rare/opportunistic visitation events by a diversity of flies (Calliphoridae, other Syrphidae), wild bees (*Ceratina* sp. and *Xylocopa* sp.) and a few butterflies (from the Pieridae, Nymphalidae, Lycanidae and Papilionidae groups).

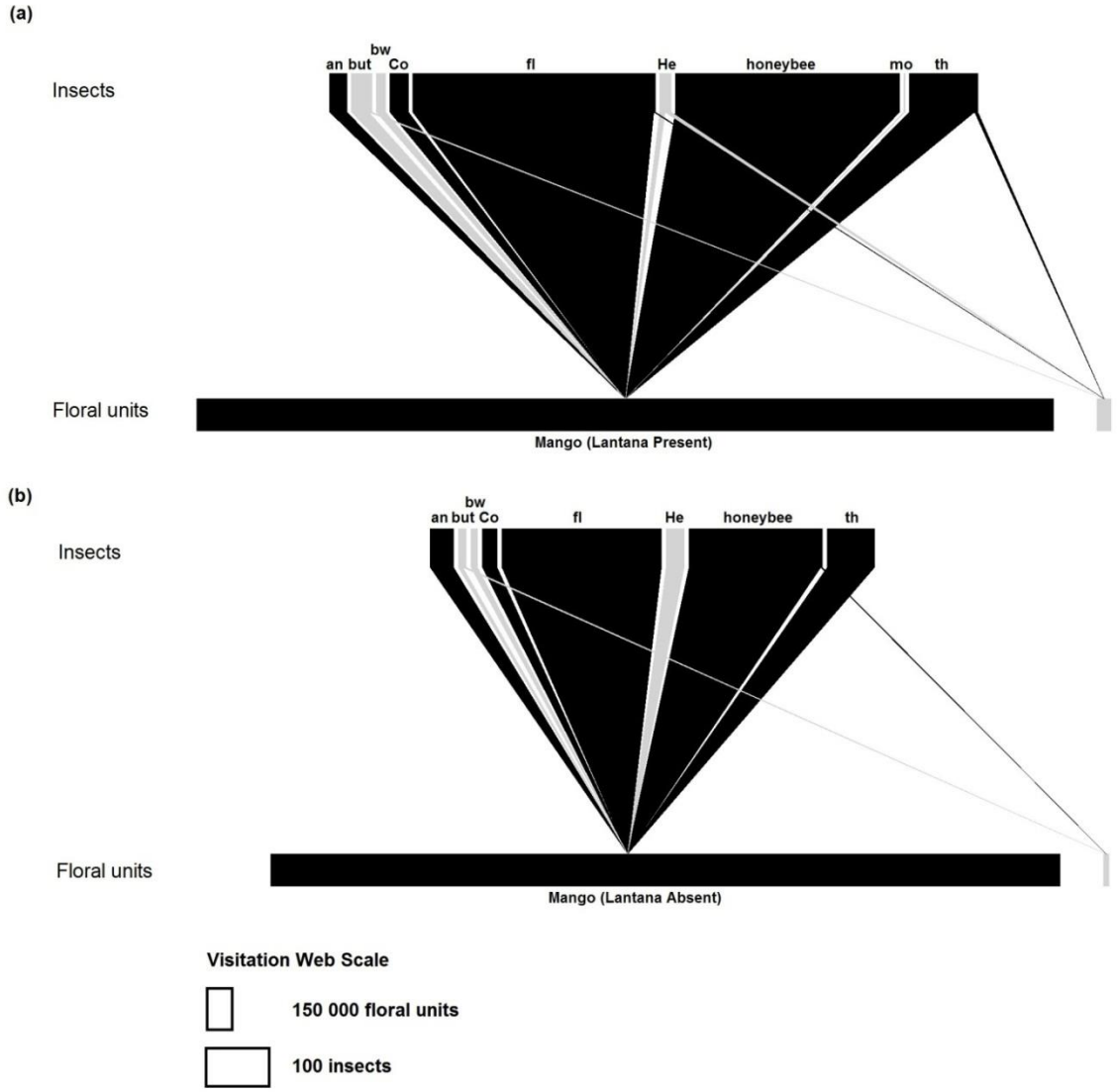

Figure 2.3. Mango flower-visitation webs of mango plots where *Lantana* is present (a) and absent (b) in nearby natural vegetation during June to October 2013. These two networks represent the total amount of interactions observed throughout all the mango study plots. Each species of plant and grouped insects are represented by a rectangle. The full species list is provided in Table A3 (Appendix 1). Rectangle width represents overall species abundance and the size of the interaction lines represent number of insects visiting each plant species. Mango and known mango pollinating flower visitors are shown in black, other flower visitors and plant species observed in plots are presented in grey. an, ants (Hymenoptera); but, butterflies (Lepidoptera); bw, other bees and wasps (Hymenoptera); Co, Coleoptera; fl, flies (Diptera); He, Heteroptera; honeybee, *Apis mellifera*; th, thrips (Thysanoptera).

Although mango flower visitation was greater for plots near *Lantana* than those without, neither mango flower visitor abundance nor species richness was significantly correlated with the floral densities of *Lantana* or other naturally occurring flowering plants (abundance: Spearman's rho = 0.162, $P > 0.05$; species richness: Spearman's rho = -0.016, $P > 0.5$). *Lantana* flower densities varied far less than that of mango (*Lantana* floral density: $\bar{x}$ = 1031, SD = 467; Mango floral density: $\bar{x}$ = 8978, SD = 6294).

All other NOFP floral densities were observed at very low densities ($\bar{x}$ = 59, SD = 66) and although small, their effect has been included in the generalized mixed models.

Overall mango flower visitor abundance was strongly correlated with mango flower density (Spearman's rho = 0.736, $P < 0.001$), and given that pollinators are known to be flower density dependent, this result is expected (Figure 2. 4). Correlations between mango flower visitor abundance for plots near natural vegetation with *Lantana* (Spearman's rho = 0.723, $P < 0.001$) and plots near natural vegetation without *Lantana* (Spearman's rho = 0.704, $P < 0.001$) showed a similarly significant and strong correlation to mango floral density.

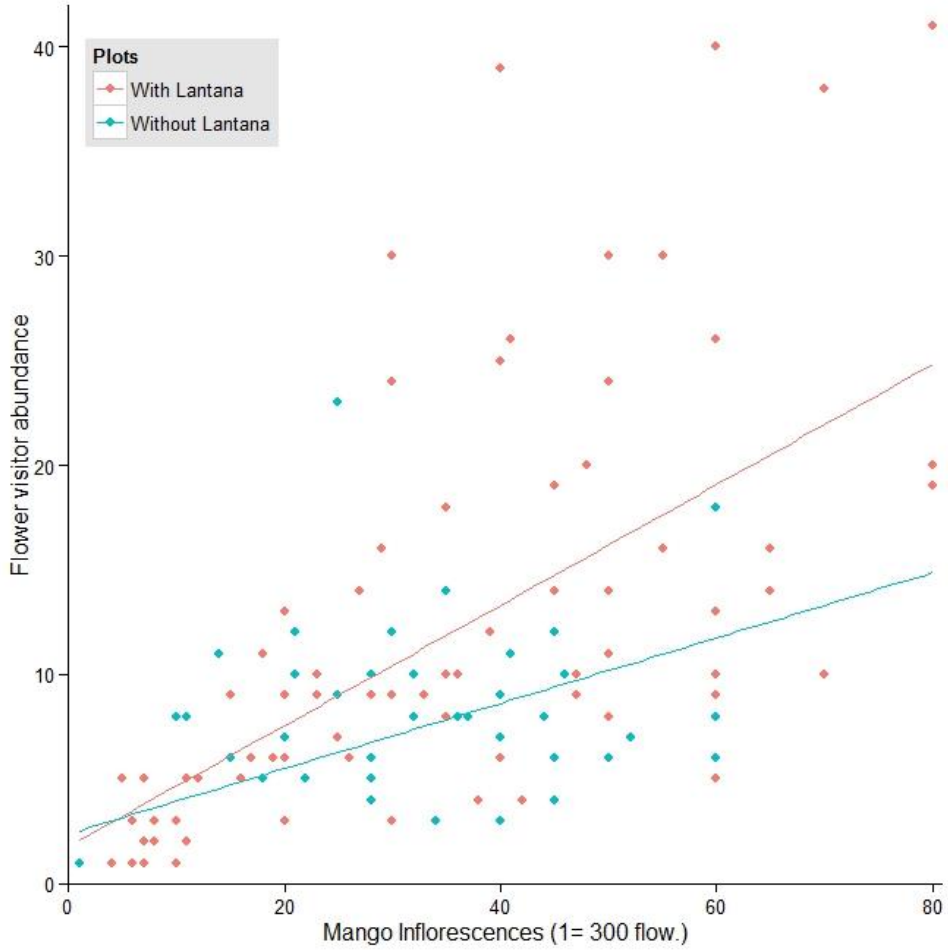

Figure 2.4. Abundance of mango flower visitors as a function of mango flower density (1 mango flower inflorescence = 300 mango flowers). The red line denotes the linear regression of flower visitor abundance to mango near natural vegetation with *Lantana* (goodness of fit (R^2) = 0.381, $P < 0.001$) and the blue of flower visitors to mango near natural vegetation without *Lantana* (R^2 = 0.394, $P < 0.001$).

Mango flower visitor species richness was significantly correlated with mango floral density in mango plots neighbouring *Lantana* (Spearman's rho = 0.712, $P < 0.001$), compared to plots that do not (Spearman's rho = -0.171, $P > 0.5$) (Figure 2.5). This indicates that *Lantana* presence is a significant factor in explaining increased visitor species richness levels in mango plots.

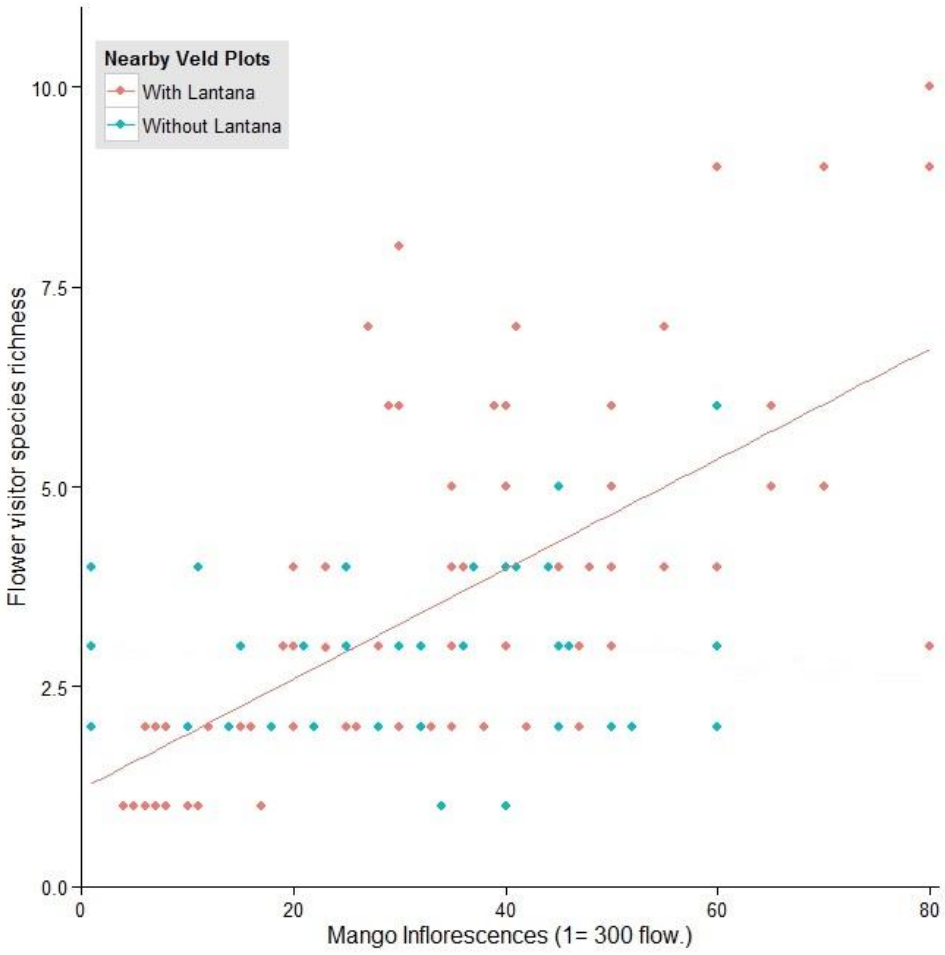

Figure 2.5. Species richness of mango flower visitors as a function of mango flower density (1 mango flower inflorescence = 300 mango flowers). The red line denotes the linear regression of flower visitor species richness to mango near natural vegetation with *Lantana* ($R^2 = 0.442$, $P < 0.001$).

The best fitting model for mango flower visitation (i.e., interaction per mango flower) finds that the floral densities of mango, NOFP and the *interaction* between *Lantana* and other NOFP (co-occurrence of nearby *Lantana* and NOFP) are significant in determining observed mango flower visitor abundance and species richness, with a marginal R^2_{GLMM} of 43,99% and conditional R^2_{GLMM} of 72,06% (Table 2.2). Thus, the effect of *Lantana* flower abundance on mango flower visitation depended on the abundance of other NOFPs, and this effect became more accentuated as the abundance of other NOFPs was

increased. The floral density of NOFPs could be erroneously identified as a contributor to flower visitor abundance as the selection criteria are sensitive to small sampling sizes, which NOFP floral density was in this study ($\bar{x}$ = 59, SD = 66). All model assumptions (of heteroskedasticity and residuals normality) were checked and satisfied during model validation.

Table 2.2. The effect of the floral density of mango, *Lantana* and NOFPs and distance to natural vegetation margin on mango flower insect visitor abundance and species richness. Results for each response variable are presented for different models. Variables in model contribute significantly to the fit of the best model (lowest AICc). Likelihood ratio tests calculated *P*-values during stepwise elimination, where models were compared for significance. 'ns', non-significant = $P > 0.05$. '-', variable not included in the model.

Response variable (*Y*)	**Mango flow. (F_1)**	***Lantana* flow. (F_2)**	**NOFP flow. (F_3)**	***Lantana* flow.*NOFP flow. (F_2F_3)**	**Distance (*D*)**	**Df**	**AICc**	**BIC**
Flower visitor abundance								
Model 1 (best model)	**< 0.001**	0.07 (ns)	< 0.01	**< 0.001**	-	9	855.9	880.9
Model 2	< 0.001	< 0.01	< 0.01	< 0.001	0.4 (ns)	9	862.5	887.2
Model 3	< 0.001	0.052 (ns)	< 0.01	-	0.3 (ns)	8	881.2	903.5
Model 4	-	<0.01	< 0.001	< 0.001	0.3 (ns)	8	927.3	949.7
Best model equation $Y = e^{1.254+0.00006F1-0.003F3+0.000007F2F3}$								
Flower visitor species richness								
Model 1 (best model)	**< 0.001**	0.3 (ns)	< 0.5 (ns)	**< 0.001**	-	9	505.6	530.7
Model 2	< 0.001	0.3 (ns)	< 0.5 (ns)	< 0.001	0.9 (ns)	9	506.5	531.2
Model 3	< 0.001	0.8 (ns)	< 0.5 (ns)	< 0.005	0.9 (ns)	9	509.5	534.5
Model 4	-	0.6 (ns)	< 0.01	< 0.01	0.7 (ns)	8	515.7	538.1
Best model equation $Y = e^{0.8976+0.00004F1+0.000006F2F3}$								

2.3.2. Does Lantana *serve as additional floral resource to mango flower visitors before and after mango flowering?*

Flower visitor community composition changed significantly with time, i.e., before (June), during (August) and after (October) mango flowering, in natural vegetation (Table 2.3).

Table 2.3. Results from the multivariate permutational analysis (PERMANOVA) of differences in flower visitor community composition based on square-root transformed abundance data between natural vegetation neighbouring mango orchards from surveys before (June), during (August) and after (October) mango flowering and plot condition (*Lantana* present or absent).

PERMANOVA	**df**	**SS**	**MS**	**Pseudo-F**
Abundance				
Survey date x condition	4	80060	20015	9.272
Residual	145	31299	2158	
Total	149	111395		
Pair-wise test	**2L**	**2NL**	**3L**	**3NL**
1L	3.54**	3.04**	2.01*	3.02***
2L		3.81*	2.86**	4.19***
2NL			2.83***	1.75**
3L				2.69**

t values shown for pair-wise tests. Surveys of natural vegetation with *Lantana* present before mango flowering (1L), during mango flowering in plots with (2L) and without *Lantana* (2NL) and after mango flowering in plots with (3L) and without (3NL) *Lantana*. Number of permutations for each analysis = 9999. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The flower visitor community assemblage of natural vegetation, before, during and after mango flowering, differed between plots with and without *Lantana camara* (canonical analysis of principal coordinates (CAP) ordination, Figure 2.6). In plots with *Lantana*, flower visitor community assemblage is similar before and after mango flowering, but different during mango flowering (Figure 2.6). Data for flower visitor community assemblage in the natural vegetation without *Lantana*, during the first survey, were not obtained as there were no flowers in the plots during the data collection in that time.

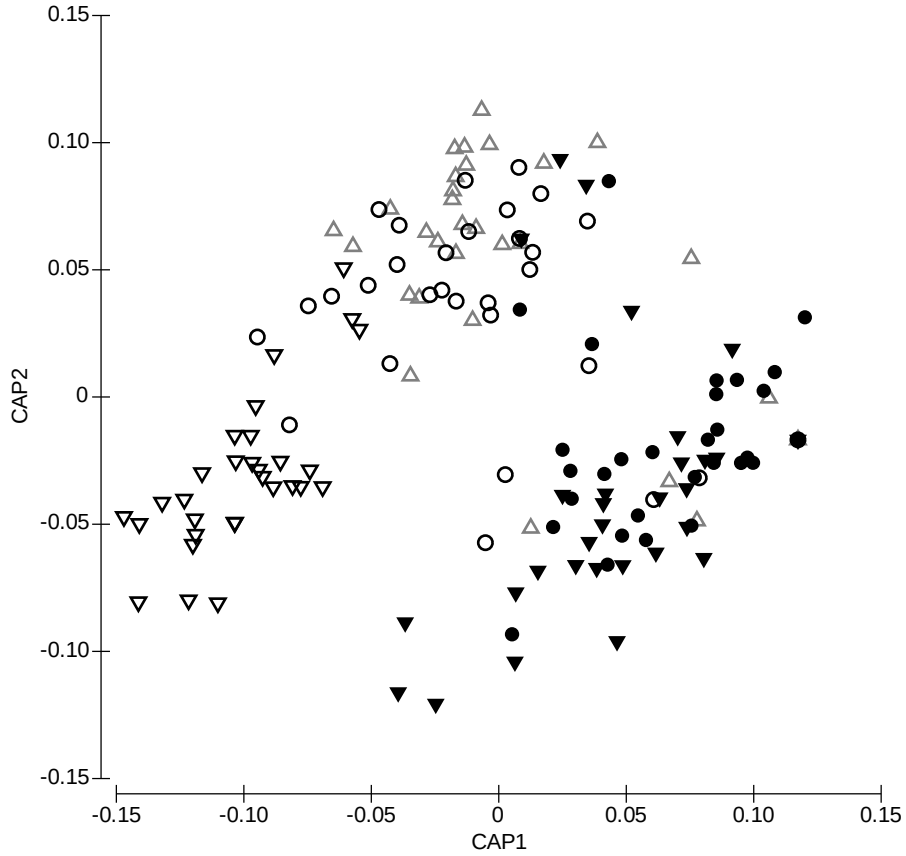

Figure 2.6. Canonical analysis of principal coordinates (CAP) ordination of the flower visitor community assemblage in natural vegetation bordering mango orchards before (June), during (August) and after (October) mango flowering season. The first survey was done only in natural vegetation with *L. camara* (open grey triangles), the second survey in natural vegetation with (empty black triangle) and without *L. camara* (black triangle) and the third survey also in natural vegetation with (empty circle) and without *L. camara* (black circle). Cross validation was at m: 11 and mis-classification error was 36.67%.

Few flower visitor species were shared between *Lantana* and mango before (7 sp.) and after (7 sp.) mango flowering, compared to during mango flowering (43 sp.). The largest change in *Lantana* flower visitation by shared flower visitors (shared with mango) was seen for *Musca* sp., *Lepisiota* sp., *Xylocopa caffra* and *Apis mellifera* (Table 2.4).

Table 2.4. The amount of *Lantana camara* flower interactions by the most common shared insect flower visitors (shared between *Lantana* and mango) before (June), during (August) and after (October) mango flowering in natural vegetation bordering mango orchards.

Flower Visitors		***Lantana* flower interactions**		
Group	*Species*	Before	During	After
Diptera				
	Musca sp. 2	119	314	105
	Musca sp. 3	5	20	3
	Syrphidae sp.*	0	8	0
	Tachinidae sp.	1	15	2
Formicidae				
	Camponotis sp.	0	6	2
	Pheidole sp.	15	2	8
	Lepisiota sp.	31	36	55
Apidae				
	Xylocopa caffra	2	81	6
	*Apis mellifera**	3	36	7
Apocrita				
	Vespidae sp.	0	15	3

* Known mango pollinating flower visitors making-up at least 10% of total mango flower visitation.

Before mango flowering (June), there were 266 insect-flower interactions by 29 species in natural vegetation. During mango flowering (July, August and September), 1312 flower visitations (on average 437 interactions) by 75 flower visitor species, and after mango flowering 579 flower-insect interactions were observed in the natural vegetation plots by 54 species (Figure 2.7). *Lantana camara*'s floral density increased from before (31 276 flowers) to during (102 965 flowers) mango flowering season, but decreased abruptly after mango flowering (6234 flowers). Flower visitation to *Lantana* after mango flowering was proportionately (interaction per flower) larger than before or during the season (Figure 2.7).

During the first period, i.e., before mango flowering, flies (143 interactions (int.)), ants (49 int.) and butterflies (64 int.) dominated flower visitation in natural vegetation plots. During mango flowering, however, flies (147 int.), ants (35 int.), butterflies (103 int.) and bees (79 int.) dominated the flower visitor community. After mango flowering, flies (138 int.), ants (103 int.) and butterflies (177 int.) still visited flowers most, including a larger portion of flower visitation by Hemipteran (106 int.) species (Figure 2.7).

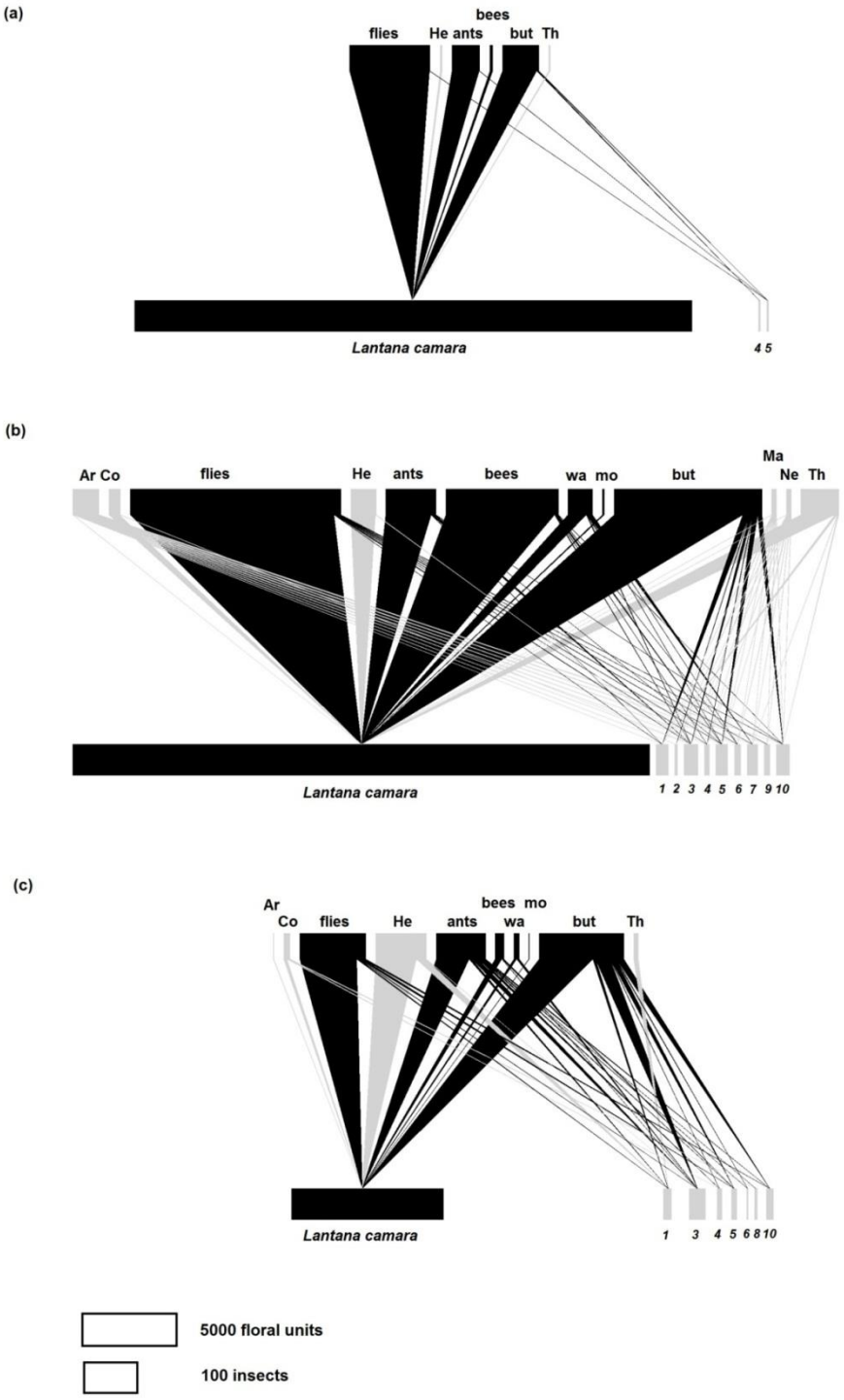

Figure 2.7. Effect of seasonal change, of (a) before, (b) during and (c) after mango flowering, to natural vegetation neighbouring mango orchards. The three plots present three surveys done in June (before), August (during), and October (after) 2013 on commercial mango farms (Bavaria, Jonkmanspruit and Mohlatsi). Each insect and plant family group/species abundance is represented by a rectangle and proportion of interactions (flower visitor individual to flower) is indicated by the size of lines connecting them. The overall list of species is provided in Table A3 (Appendix 1). *Lantana camara* and known *Lantana* pollinators are shown in black and other flower visitors and plant species observed in plots are presented in grey. Ar, Araneae; Co, Coleoptera; flies, Diptera; He, Heteroptera; ants, Formicidae (Hymenoptera); bees, Apoidea (Hymenoptera); wa, wasps, Apocrita (Hymenoptera); mo, moths (Lepidoptera); but, butterflies (Lepidoptera); Th, thrips (Thysanoptera).

2.4. DISCUSSION

2.4.1. Does **Lantana** *compete with or facilitate mango flower visitation?*

Here, the expectation that *Lantana camara* shared flower visitors with mango proved to be true, although *Lantana* did not compete for flower visitors with mango. Instead, facilitation effects have been identified whereby increased visitation by a larger diversity of insects is seen on mango flowers in close proximity to *Lantana* and other naturally occurring flowering plants in bordering natural vegetation. Mango flower density was correlated to mango flower visitor abundance. Herrmann *et al.* (2007) found similar results of an increase in bumblebee (*Bombus* sp.) abundance in agricultural areas because of greater resource availability provided by mass flowering crops (see also Hanley *et al.* 2011; Holzschuh *et al.* 2013; Westphal *et al.* 2003). *Lantana*'s involvement in increasing both mango flower visitor abundance and species richness could be ascribed to its creating a "magnet effect" (attraction mechanism) by forming a large part of the collective floral display when little else is flowering, while co-occurring in habitat bordering mango orchards (Feldman *et al.* 2004; Rathcke 1983). The additional increased availability of attractive floral resources presented by *Lantana* and a few NOFPs lure insects from the wider surrounding area to visit the less-appealing co-flowering mango flowers (Carvalheiro *et al.* 2010, 2012). This result corresponds with several other studies on highly rewarding flowering plants facilitating pollination of co-flowering plants (see Duffy & Stout 2011; Johnson *et al.* 2003; Moeller 2004; Sieber *et al.* 2011).

Overall pollinator abundances may prove to be more important to mango flower visitation than we think. Ye *et al.* (2014) found that larger pollinator abundances resulted in increasing flower visitation with the increased floral densities of two plants, *Lotus corniculatus* and *Potentilla reptans*, whereas no relationship between visitation rates and floral density was found at low pollinator abundance. The implications of this are that low pollinator abundances may not lead to accelerated flower visitation by pollinators on mass flowering crops (such as mango) and that higher abundances contribute to more successful flower pollination (and therefore fruit production).

Similarly, pollinator species diversity is important to mango flower visitation and fruit production. Different pollinator species present a variety of behaviours and body sizes which determine foraging height levels, and the time of day and season they are most active (Hoehn *et al.* 2008). The importance of pollinator species richness is noted by Greenleaf & Kremen (2006), who found that a higher diversity of visitor species increased the pollination effectiveness of flying pollinators through the promotion of movement between flowers due to inter-specific interactions.

2.4.2. Does **Lantana** *support mango flower visitors before and after mango flowering?*

Here it could not be fully determined whether *Lantana* provided additional food resources to mango flower visitors. Flower visitor species show that fewer known mango flower visitor species visited *Lantana* before and after mango flowering (7 out of 24 species before and 7 out of 47 species after mango flowering) compared to their amount (43 out of 119 species) during mango flowering. The species that visited *Lantana* before and after mango flowering mainly consisted of *Musca* sp., Syrphidae sp., Tachinid sp., *Camponotis* sp., *Pheidole megacephala, Lepisiota* sp., and *Apis mellifera*. This would suggest that *Lantana* is not a primary floral resource to many mango flower visitors either before or after mango flowering.

Flower visitor species visitation to *Lantana* increased by 92% from before to during mango flowering, where it decreased by 89% after mango flowering. *Lantana*'s flower visitor community assemblage changed dramatically over the mango flowering season. A very small flower visitor community had been visiting *Lantana* before mango flowering during June 2013 compared to the visitation rates *Lantana* experienced during flowering time (August). This community's increase in species richness and abundance of flies, ants, bees, wasps and butterflies indicates that *Lantana camara* may be part of a mutually beneficial relationship while co-occurring with mango flowers. Mass flowering crops are known to have a pollinator 'spill-over' effect for native plants in bordering natural vegetation, and here *Lantana* seems to be benefiting from it (Hanley *et al.* 2011).

Lantana's life cycle is predominantly determined by environmental conditions, with rain playing a central role in its proliferation (Sharma *et al.* 2005; Vardien *et al.* 2012). During the period after mango flowering (October to November 2013), most *Lantana* plants in the study plots senesced and did not regrow during the last months of field work, considerably reducing its floral presence in the natural vegetation. As such, less flower visitors were seen visiting *Lantana* flowers, but this decreased flower visitation may also be caused by natural variation in visitor behaviour and fluctuation in community size (after mango flowering there are fewer food resources available). Sydenham *et al.* (2014) found great variation in solitary bee species composition in field edges throughout the year, which varied mainly due to environmental conditions and floral density. Other ecological studies on flower visitor communities indicate significant seasonal variation in flower visitor species richness and abundance due to temporal fluctuations as well as changes in patterns of flower preference, which may also be the case in this study (see Oertli *et al.* 2005; Richards *et al.* 2011).

Lantana, then, provides facilitation to mango flower visitation which could lead to increased mango pollination success and fruit yield, as a greater diversity of flower visitors has been shown to increase mango fruit set (Carvalheiro *et al.* 2010; Garibaldi *et al.* 2013). Initially, this may present a contradiction as reviews of the impacts alien plants ultimately have on native pollination networks conclude that,

more often than not, alien plants, especially *Lantana*, exercise negative effects on pollination services and reproductive success (seed-set) of native plants in comparison to uninvaded areas (Morales & Traveset 2009; Pyšek *et al.* 2012). Furthermore, the negative impacts of alien invasives on pollination and reproductive success of co-flowering plants increases exponentially with increased relative alien plant abundance (Dietzsch *et al.* 2011; Flanagan *et al.* 2010; Morales & Traveset 2009; Waters *et al.* 2014). Whereas studies have shown strong negative effects of invasive plants on the pollination and reproductive success of native plants (Brown *et al.* 2002; Chittka & Schurkens 2001), a few have reported that IAPs also offer a facilitative component to their invasive capabilities (Carvalheiro *et al.* 2014; Lopezaraiza-Mikel *et al.* 2007; Nielsen *et al.* 2008), usually at the onset of invasion or at low abundance (Muñoz & Cavieres 2008).

Plant-plant interactions through shared pollinators have been known to change over time and changes in their floral abundances often determines the effects they have on one another (Larson *et al.* 2006; Moragues & Traveset 2005; Padrón *et al.* 2009). Muñoz & Cavieres (2008) found the alien herb *Taraxacum officinale* to have a facilitative effect on the pollinator visitation of two native plants, *Hypochaeris thrincioides* and *Perezia carthamoides*, at low abundance which changed to competitive effects on pollination at higher abundances. During other times an invasive alien plant may have mixed effects on the different flowering plants occurring around it, such as that seen in Moragues & Traveset (2005), where the effect of a *Carpobrotus* sp. on the pollinator visitation of native species ranged between competitive (on *Lotus cytisoides*), facilitative (on *Cistus salviifolius* and *Anthyllis cytisoides*) and no effects (on *Cistus monspeliensis*). *Lantana* could be at too low densities for its potential negative effects on mango flower visitation to be noticed, and with mass mango flower abundances such competitive effects may not exist. At low mango flower abundance and higher *Lantana* floral abundance, competitive effects may exist between mango and *Lantana*, also, possibly with other native plants co-occurring in the natural vegetation. The mere occurrence of *Lantana* flowers has provided an increase in the amount and diversity of flower visitors to mango, particularly that of honeybees, flies (i.e., syrphids) and butterflies. This could be important to the production of mango fruit as Carvalheiro *et al.* (2010) found that honeybees alone didn't increase fruit set of mango, but that ants and flies had a significant contribution as well.

Matching the ecological structural manipulation ability of invasive plants like *Lantana* and the changing nature of habitats and pollinator foraging behaviour, *Lantana*'s effect on mango flower visitation may alternate between facilitation and competition at different floral densities (Lázaro & Totland 2010; Lázaro *et al.* 2013). As an open system, agricultural environments are prone to fluctuating abundance of alien plants, floral diversity and pollinator population structure and functioning. This creates a variety of context dependant environments for alien invasives to exercise their invasive capabilities in (Padrón *et al.* 2009; Schweiger *et al.* 2010; Traveset & Richardson 2006). Also, *Lantana*'s integration into this

complex agricultural flower visitation network could indicate the initiation of 'invasional meltdown', a state of facilitated alien infiltration and proliferation through the consequential effects of the original introduction of an alien invasive into a natural system (Simberloff & Von Holle 1999; Bourgeois *et al.* 2005). Indeed, this area is already known to be infested with a variety of other invasive alien plants and many, such as Syringa berry trees (*Melia azedarach*) and Prickly pear (*Opuntia ficus-indica*) observed on the study farms (*pers. obs.*), and may be contributing to this 'meltdown' state. Although *Lantana* may contribute to increased mango flower visitation on mango orchard boundaries, its final effect on mango flower visitation and health of adjacent natural vegetation once fully established will be extremely detrimental, as that of an intensely invasive plant.

Lantana's facilitative service adds merit to the growing concern on the integration of exotic plants into native pollination networks, especially those of agricultural importance. The danger to *Lantana*'s facilitative capability is that, while facilitative effects are in place, farm managers may shy away from their responsibility of removing and keeping their land clear of invasive alien plants. One key characteristic to *Lantana*'s pervasiveness as an invasive is its ability to transform the habitat it occurs in, through allelopathic and accelerated growth and reproductive rates it can quickly outcompete native plants (Sharma *et al.* 2005; Vardien *et al.* 2012). If such advanced invasion were to take place here it could lead to the modification of ecosystem processes, such as pollination, to better suit its invasive needs. Specialist pollinators may be negatively affected by reduced resources of native flora, which are being displaced and out-competed, as they cannot use the new resources offered by IAPs (McKinney 1997). Pollinators may also be affected by the unavailability of native plants important to their reproductive processes at different times of the year (Rathcke 1983). If this were the case, only the most generalist pollinators will be able to use the new floral resource, lowering the general abundance and diversity of pollinators, now known to be very important to mango pollination (Lopezaraiza-Mikel *et al.* 2007; Padrón *et al.* 2009).

Certain non-pollinators have been included in the visitation networks to provide information on the general interactions between insects and flowers. Some of these, i.e., Araneae, Mantodea and Neuroptera, are known to be predators of pollinators and as such, may have an effect on flower visitor foraging behaviour. This short-term study is limited to strictly understanding the effect of an alien plant on mango flower visitation and although closely linked to the pollination process, further work would be needed to determine whether successful pollination and increased fruit set are necessarily an outcome of greater visitor abundance associated with *Lantana*. Furthermore, the effect of the presence of *Lantana* on mango may not extend far into the orchards, and the effect of distance on flower visitation between *Lantana* and mango would also need to be assessed. The pollination status of flower visitors or specific pollen deposition and its effects on fertilisation and fruit production (factors vital to understanding the end result of visitation) remain to be investigated.

Management Recommendations and Future Research

Lantana should not be kept on as a beneficial plant for mango fruit production, given its highly publicised invasional status, loss of grazing potential and allelopathic effects, and difficulty in removing such communities once fully established. In economic terms, any benefit afforded to mango fruit production of a few trees on orchard margins (such facilitation may not extend far into the orchards) would be outweighed by the management costs to control *Lantana* when its densities became uncontainable, as well as the loss of grazing value of invaded adjacent natural veld (Vardien *et al.* 2012). It is important, however, to understand how these services may be affected if *Lantana* were to be removed as it could lead to a decline in mango flower visitor abundance and species richness on orchard boundaries. Due to mango's low fruit output per inflorescence (one to three fruits), such loses may not be detrimental to pollination success and fruit production. Thus, it would be unwise to maintain its floral presence within and around agricultural farmland.

Lantana's reproductive fitness (i.e., seed set) increases with cross-pollination, which is facilitated by flower visitation (Goulson & Derwent 2004). Improved seed set makes more seeds available for dispersal by birds, increasing the rate at which *Lantana* spreads (Sharma *et al.* 2005; Vardien *et al.* 2012). *Lantana* is difficult to remove once fully established in semi-disturbed areas such as those surrounding the mango orchards (Vardien *et al.* 2012). Therefore, if *Lantana*'s flower visitation is facilitated by mango flowers, *Lantana camara* bushes should be completely removed from areas bordering mango, to help prevent its spread. This also falls in accordance with the requirement to remove invasive alien plants from agricultural land as set out by the Conservation of Agricultural Resources Act, 1983 (Act No 43 of 1983) (CARA).

Appropriate surrogates can be found to replace and compensate for the missing facilitative services of the removed *Lantana* by the identification and cultivation of native flowering plant species (occurring in the same natural vegetation in the area) that also facilitate mango flower visitation. Experiments and observational studies could reveal suitable native plant floral densities necessary to facilitate mango flower visitation. Carvalheiro *et al.* (2012) has already identified native plant species of *Aloe greatheadii* ("Transvaalalwyn") and *Barleria obtusa* (Bush violet) which facilitate mango visitation by increasing species richness and abundance. Through this, the preservation of small natural vegetation fragments where NOFPs occur will initiate natural increases in mango flower visitor abundance and diversity, leading to maximized mango fruit yields (Carvalheiro *et al.* 2012).

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Chapter 3. Flower visitor communities in mango orchard boundaries and neighbouring natural vegetation

- Differences in assemblage composition and species richness -

ABSTRACT

Pollination is a vital ecosystem service, which can be disturbed by environmental changes, such as the establishment of agricultural crops and invasive vegetation. Flower visitor communities in natural vegetation adjacent to animal-pollinated crops play a central role in ensuring crop pollination, yet very little information is available on their dynamics and structure. In commercial mango orchards in Hoedspruit, South Africa, mangoes are pollinated by a wide diversity of insects that are supported by bordering natural vegetation. Mango shares several flower visitors with natural flowering plants and *Lantana camara*, an invasive alien plant in natural vegetation which has similar floral characteristics to mango and flowers year-round. Here, I determine whether the composition of insect flower-visitor community assemblages differ between mango orchard margins and neighbouring natural vegetation, and how the presence of *L. camara* affects these assemblages. Flower visitation surveys were conducted in natural vegetation plots bordering mango orchards and mango orchard boundary plots before, during and after mango flowering. Flower visitor community compositions and species turnover were assessed, and flower visitor networks constructed. There was a significant difference between flower visitor community assemblages in mango orchard vs. natural vegetation, and where *L. camara* was present, community structure changed in both mango and natural vegetation. Flower visitor communities were largely influenced by large abundances of flowers of the alien invasive shrub, *Lantana camara*, possibly indicating a successful invasional pathway.

3.1 INTRODUCTION

Key ecosystem services are affected by global change pressures, such as landscape alteration, non-native species, climate change and agricultural intensification (González-Varo *et al.* 2013). One such crucial ecosystem service, pollination, is particularly vulnerable as slight environmental disturbances can have major negative effects by diminishing the function of this service (Kennedy *et al.* 2013; Kremen & Ricketts 2000; Potts *et al.* 2010). Recently, with the continued pressure on natural ecosystems, there have been major global declines in crop pollinator populations and their services which have led to decreased seed set in native plant species and lower crop yields (Johnson 2010; Vanbergen & IPI 2013). Lower yields of crops important in human diets, i.e. fruit and vegetables, highlights the threats that continued declines in pollination services pose to human nutrition (Eilers *et al.* 2011; Gallai *et al.* 2009). In light of these declines, crop management focussing on the recovery of native pollinator biodiversity and rehabilitation of pollination services have been recommended to improve overall agricultural production and boost yields of pollinated crops (Dicks *et al.* 2013; Garibaldi *et al.* 2014).

The conservation of functionally-important pollinating insects is crucial for a stable supply of pollination services (Jackson *et al.* 2007; Kremen 2005; Steffan-Dewenter & Westphal 2008). The importance of diversity and abundance of wild pollinators has been largely underestimated in the past and has now become a central focus of pollination studies in agricultural production (Carvalheiro *et al.* 2011; Garibaldi *et al.* 2013; Hoehn *et al.* 2008; Holzschuh *et al.* 2013; Kennedy *et al.* 2013). With the ever-increasing demand for pollination services in agriculture, management and promotion of wild pollinators are now considered as essential as managed honeybee colonies (Aizen & Harder 2009; Garibaldi *et al.* 2013; Greenleaf & Kremen 2006). The advent of Colony Collapse Disorder (CCD), which has affected approximately 35% of managed honey bees in the U.S.A, U.K. and Europe, has highlighted the danger of relying on a single species to meet agricultural pollination needs (Aizen *et al.* 2008; Johnson 2010; Potts *et al.* 2010; Vanbergen *et al.* 2014;). Furthermore, a diverse set of wild pollinators is linked to better seed set and pollination efficiency than honeybee pollination alone (Garibaldi *et al.* 2013). Therefore, more knowledge and understanding of native pollinating communities found within and bordering farmland can guide management practices ensuring pollinator proliferation, which would help meet pollination needs.

Increased size and improved quality of natural vegetation areas provide more food and nesting resources for wild pollinators, boosting their species richness and abundance (Garibaldi *et al.* 2011; Winfree *et al.* 2008). Carvalheiro *et al.* (2012) established small patches of native flowers along mango orchard boundaries on commercial mango farms near Hoedspruit that resulted in increased flower visitation to mango by a wider diversity of pollinating insects, improving fruit yield. Furthermore, native pollinators travel into agricultural areas to visit nearby crop flowers, a phenomenon referred to as a pollination 'edge effect' or 'spill-over effect' (Blitzer *et al.* 2012; Chacoff & Aizen 2006), but there is little information on whether the reverse is true, i.e., that pollinating insects move from agriculturally-managed areas into neighbouring natural vegetation (Blitzer *et al.* 2012). It is likely, however, that flower visitors from farmland do cross over into natural habitat to visit naturally-occurring flowering species (Lander *et al.* 2011). Generally, it seems as if pollinating insects from natural areas forage around crops to supplement their food resource needs, and return to the natural areas where they complete their reproductive cycle, as it provides a more stable habitat than frequently disturbed farmland (Blitzer *et al.* 2012; Greenleaf *et al.* 2007; Holzschuh *et al.* 2007).

Improving the abundance and species richness of native pollinators requires knowledge about their community structure, i.e., species composition and abundance, and how this is influenced by habitat type (Garibaldi *et al.* 2013, 2014). The community structure, species richness and abundance of functionally important pollinators, such as bees, are closely linked to nectar resource diversity and floral abundance and diversity (Potts *et al.* 2003). Different pollinator communities are found within managed,

semi-managed and natural areas due to differences in floral assemblage (nectar resource diversity), which affects the presence of specific pollinators (Potts *et al.* 2003; Stachowicz 2001).

Working in mango orchards in Hoedspruit, South Africa, Carvalheiro *et al.* (2010) found that flowering plants in bordering natural vegetation shared flower visitors with mango (Figure 3.1). This same study showed that mango pollination is largely dependent on native pollinating insects, and less so on the managed honeybee colonies (*Apis mellifera*) introduced into orchards during mango flowering season (Carvalheiro *et al.* 2010, 2012). In Chapter 2, it has been established that the presence of *Lantana camara* (hereafter referred to as *Lantana*) in the nearby natural vegetation is associated with increased flower visitor abundance and species richness to mango during mango flowering. The apparent relative importance of native vegetation bordering mango, and mango pollination's dependence on native pollinators, seems to depend on the composition of flower visitor communities in both the agricultural and neighbouring natural areas.

Given differences in habitat types for pollinators, and in particular, nectar resource diversity, nectar energy content, nesting substrate availability, floral abundance and diversity, I will ascertain (1) whether flower visitors to mango at orchard edges are significantly different to those found in natural vegetation bordering mango orchards, and (2) how *Lantana camara* influences flower visitor communities in both these areas. I expect the flower visitor communities of mango orchard and natural vegetation to be quite distinct from one another due to differences in floral community composition. This study will shed some light on the invasive integration pattern, and consequences thereof, of an invasive alien plant *Lantana camara* on an agricultural network and contribute to our understanding of the underlying native pollinator community structure servicing mango pollination. This information will guide management on how best to benefit native pollinator communities for mango crop pollination.

3.2. METHODS

3.2.1 Study area and design

Flower visitation data were collected on three (Bavaria, Jonkmanspruit and Mohlatsi) commercial mango farms near Hoedspruit, Limpopo, South Africa. Five flower-visitor surveys were conducted monthly between June to October 2013. These farms share similar management practices for pesticide application (neonicotinoids or organophosphates), irrigation, harvesting period, cropping system, removal of flowering plants growing mango orchards, and the use of managed honeybee colonies as supplement to pollination during mango flowering, with minimal variation in abiotic factors (i.e., soil, sunlight exposure and climate). In the study sites, mango orchards are bordered by large areas of natural vegetation (Granite Lowveld; Mucina & Rutherford 2006), in which invasive alien plants, such as *Lantana camara*, have become established in some parts.

Flower visitor surveys consisted of observing insect flower visitation within fixed plots, either in mango orchard boundaries or in neighbouring natural vegetation. Twenty paired observational plots per farm (i.e., 120 plots in total) were located across mango orchard-vegetation boundaries. Each pair consisted of a mango plot matched with a plot in neighbouring natural vegetation (within 15m from one another). I noted whether or not *Lantana camara* was present or absent in plots of natural vegetation and which mango cultivars were in mango plots (these were Keitt, Kent, Sensation, Shelly and Tommy Atkinson). Pairs of plots were situated at least 100 m away from each other, and at least 150 m from large water bodies.

Figure 3.1. *Lantana camara* (left) and mango, *Mangifera indica*, (source: http://www.nature-onstatia.com/mangifera%20indica1.jpg) (right) flowers share similar floral traits, such as their small size, white, yellow and pinkish colouring and are known to share some pollinators (as found in Chapter 2).

3.2.2. Flower visitation surveys

Surveys were done on warm (20 – 39 °C), dry days with little wind (0 – 4 km h^{-1}) between 08h00 and 16h00 (Figure 3.2). Two observers stood at opposite points of a plot (2 x 2 m) looking in, recording all insect interactions with flower heads for 20 minutes. Insect and plant species, visitation frequency of specific species and floral density (individual flowers per unit area) of each flowering plant occurring within the plot were noted. In the natural vegetation, individual flowers were counted for floral density, whereas in the mango, given its mass floral densities, floral density was calculated by averaging the floral count of three inflorescences (± 300 flowers) and multiplying it by the number of inflorescences present within the observational plot. An individual of every flower visitor species observed was sampled for identification purposes (done under the Limpopo Provincial Government Permit No. 001-CPM401-00005, issued on 14/06/2013). Flower visitation, or the interaction between an insect and flower, is defined as the movement of a potential pollinator on or in the flower tube where it is possible that the insect has come into physical contact with flower stamens or stigma, potentially leading to pollen transfer.

Flower visitation surveys done before and after mango flowering (i.e., in June and October 2013) in the natural vegetation included the focal species, *Lantana camara*, Daisy sp., *Jasminum multipartitum* (wild jasmine), *Justicia flava*, as well as other non-indigenous flowering plants (also considered to be naturally occurring flowering plants, NOFPs) such as *Bidens pilosa* (Blackjack), *Tridax procumbens*, *Melia azedarach* (Syringa), *Onopordum acanthium* (Scotch thistle), and *Ipomoea purpurea* (common morning glory). During the winter mango flowering (July to September, beginning October), however, few plants were flowering in the natural vegetation, and the flowering community was dominated by *Lantana camara*, *Ipomoea purpurea* and *Tridax procumbens*. Managed honeybee colonies (*Apis mellifera scutellata*) were placed at densities of approximately one hive per hectare within orchards during the mango flowering period.

Figure 3.2. (a) A flower visitor (African common white butterfly, *Belenois creona severina*) on a *Lantana camara* flower, (b) the mango orchard boundary in full flower at Bavaria fruit estate, (c) dense *Lantana camara* growth neighbouring mango orchards before mango flowering and (d) the same mango orchard boundary after flowering and after *Lantana camara* had senesced.

3.2.3. Species Estimator Indices, statistical analyses and ecological networks

ICE (Incidence Coverage-based Estimator), Chao2 and Jacknife2, as non-parametric species estimators, were calculated to determine sampling efficiency and estimated species richness (Chazdon *et al.* 1998; Colwell & Coddington 1994; Hortal *et al.* 2006). All species richness estimations were calculated using EstimateS (Colwell 2009).

Beta-diversity of flower visitor communities were assessed in two ways (following Pryke *et al.* 2013); (β1) within a factor and (β2) between factors. Pryke *et al.* (2013) have defined the classifications of both as (β1) "species turnover among similar sites" (e.g., among natural vegetation; Anderson 2006) and the (β2) "assemblage compositional changes between factors" (e.g., between natural vegetation and mango) (Pryke *et al.* 2013). The two diversity measures were compared for the two plot areas (natural vegetation and mango) with different conditions (*Lantana camara* absent or present).

Permutational multivariate analyses of variance (PERMANOVA) in PRIMER 6 (PRIMER E 2009) was used to determine similarity of the flower visitor assemblage (in terms of abundance, β2) between plot

(natural vegetation and mango orchard boundary) and condition (*Lantana camara* absent and present). Data were square-root transformed to increase weight of rare species and their similarities were assessed using Bray-Curtis measures (Anderson 2001). Differences between the mango plots (with and without *Lantana*) and natural vegetation (with and without *Lantana*) were assessed by obtaining F- and *P*-values from pairwise tests, with 9999 permutations used during all analyses.

Presence/absence data was used in PERMDISP analyses (with Sørensen similarity measure) to determine the degree of variability (distance to centroid of group) in flower visitor species composition within the mango (with and without *Lantana*) and natural vegetation (with and without *Lantana*) plots by testing the similarity of multivariate dispersion (spread of flower visitor community relatedness) ($\beta 1$) in PRIMER 6 (PRIMER E 2009). As this test compares community structure/dispersion (species presence and absence data) and variation in flower visitor assemblage composition between factors across the four different areas (all found in different locations), it is used as an indication of beta-diversity (Anderson 2006).

Post-hoc analysis of plot and condition were done using canonical analysis of principal coordinates (CAP), whereby particular gradients of interest in a multivariate dataset may be outlined in plot form (Anderson 2008; Anderson & Willis 2003).

Flower-insect visitation webs were constructed as graphical tools to aid visualisation of insect-plant interactions, from pooled visitation data (of mango, *Lantana* and NOFPs) of all 60 paired plots in natural vegetation and mango orchard boundaries, using the R Bipartite package (Dormann *et al.* 2009). Visitation webs of mango orchard and natural vegetation are presented to aid visualisation of flower visitor communities between these two areas. Information regarding the status of flower visitors as mango and *Lantana* pollinators have been determined from published literature and field guides (Barros *et al.* 2001; Barrows 1976; Chin *et al.* 2010; Goulson & Derwent 2004; Hamm 2012; Louw & Labuschagne 2011; Muthoka & Mananze 2005; Sharma *et al.* 2005; Waite 2002).

3.3. RESULTS

3.3.1. Flower visitor assemblage composition, species richness and abundance in natural vegetation and mango orchard boundaries

In total, 3625 flower visitor-plant interactions were observed by 122 flower-visiting species, during the five surveys on the three farms. The highest number of interactions was in natural vegetation, with 2157 interactions by 92 flower-visiting species, compared to 1468 insect-flower interactions by 76 flower-visiting species in mango plots (Table 3.1). Plots in mango with *Lantana* absent had the lowest number of flower-visiting species but mango plots with *Lantana* present had the highest species richness estimates (Table 3.1). Both natural vegetation and mango with *Lantana* had more species when corrected for number of individuals than when *Lantana* was absent. Overall, flower visitor species consisted of 12 Coleoptera, 30 Diptera, 13 Hemiptera, 19 Hymenoptera (5 bee and 14 wasp spp.), 31 Lepidoptera (3 moth and 28 butterfly spp.), and 9 Formicidae species, as well as a further 6 species from other orders.

Table 3.1. Species estimates for the overall, natural vegetation and mango assemblages (with and without *Lantana camara*).

Area	**Obs. spp.**	**Individuals**	**ICE**	**Chao2**	**Jack2**
Overall	120	3625	152.19	155.82 (SD ± 16.34)	171.55
Natural vegetation with *Lantana*	87	1779	114.91	109.02 (SD ± 11.14)	123.88
Natural vegetation without *Lantana*	53	378	71.36	65.46 (SD ± 7.5)	76.48
Mango with *Lantana*	64	1003	172.82	199.41 (SD ± 70.57)	136.49
Mango without *Lantana*	33	465	45.56	53.42 (SD ± 15.91)	54.1

Observed species (Obs. spp.) and number of individuals (Individuals) are also given for all groups sampled. ICE = Incidence-based Coverage Estimator, Chao2 = second order Chao estimator, Jack2 = second order Jackknife estimator.

Flower visitor community composition differed significantly between natural vegetation and mango orchards. The presence of *Lantana camara* was also associated with significant differences in species composition for both natural vegetation and mango (Table 3.2).

Table 3.2. Results from the multivariate permutational analysis (PERMANOVA) of differences in flower visitor community composition based on square-root transformed abundance data, between plot location (natural vegetation or mango orchard) and condition (*Lantana* present or absent).

PERMANOVA	df	SS	MS	Pseudo-F
Abundance				
Plot x Cond	3	12587	4195	23.646
Residual	116	20582	1774.4	
Total	119	33169		
Pair-wise test (t values)	NV-L	M+L	M-L	
NV+L	3.62***	6.46***	6.24***	
NV-L		5.08***	4.45***	
M+L			2.60**	

NV natural vegetation neighbouring mango orchards, *M* mango orchard boundaries in close proximity to natural vegetation with (+*L)* or without (-L) *Lantana camara*. Number of permutations for each analysis = 9999. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species turnover was highest in natural vegetation plots, particularly when *Lantana* was absent (more variation in flower visitation by different flower visitors, see Table 3.3) and mango plots with *Lantana* present show the least amount of turnover (less variation in flower visitation by different flower visitors) (Figure 3.3). Natural vegetation flower visitor community assemblage was significantly different with the presence and absence of *Lantana*, and, although significantly different, mango plots with and without *Lantana* had more similar community assemblages to one another than to natural vegetation (Figure 3.4).

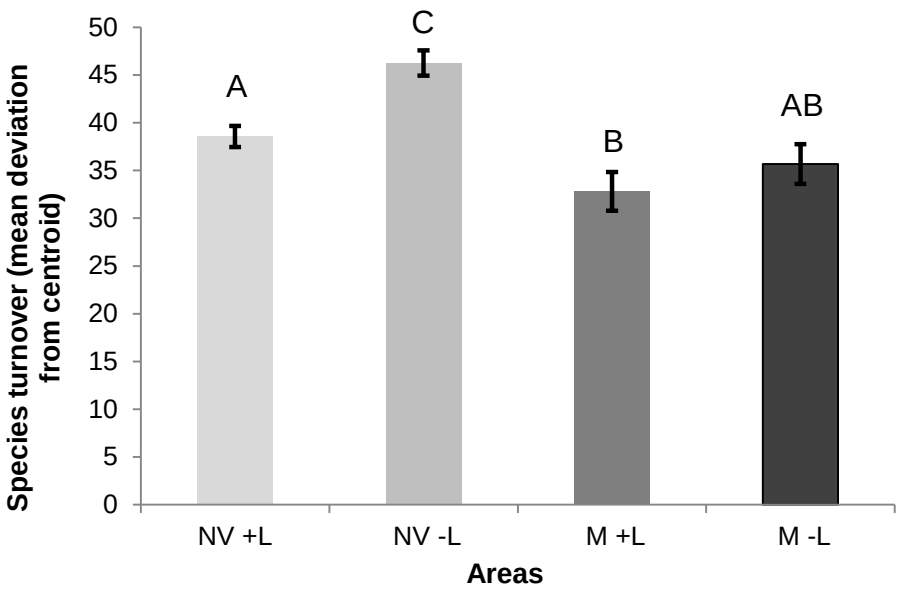

Figure 3.3. Mean species turnover (± SE, standard error) among similar sites between natural vegetation plots with *Lantana* (NV +L) and without *Lantana* (NV –L), and mango orchard plots with *Lantana* present in close proximity (M +L) and *Lantana* absent (M –L). Different letters above bars represent significant differences in flower visitor species turnover between two areas ($P < 0.05$).

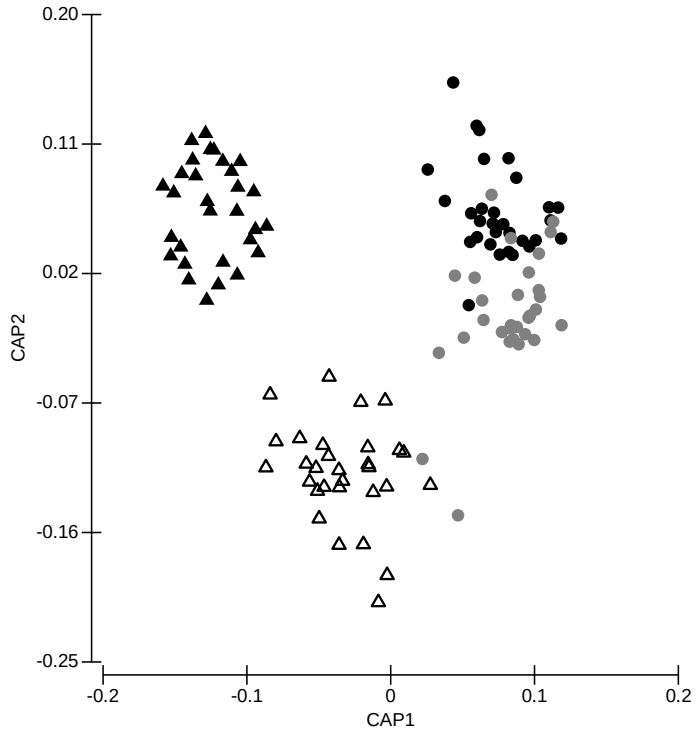

Figure 3.4. Canonical analysis of principal (CAP) coordinates ordination of the flower visitor assemblage between plot and condition elements: natural vegetation with *Lantana* (black triangle), natural vegetation without *Lantana* (open triangle), mango orchard boundaries with *Lantana* present (black circle), and mango orchard boundaries with *Lantana* absent (grey circle). Cross validation was at m: 14 and mis-classification error was 8.33%.

The greatest differences in total NOFPs flower visitor abundance were seen for Lepidoptera (Coliadinae and Pierinae sp.) [82% decrease], Diptera (Muscidae and Tachinidae sp.) [96% decrease] and ants (*Lepisiota* sp.) [93% decrease] between natural vegetation plots where *Lantana* was present and absent (Table 3.3). Such changes in abundance should be evaluated along with the differences in floral densities between natural vegetation plots with and without *Lantana* (NOFP floral density found within plots with *Lantana*, $\bar{x}$ = 818 flowers (fl.), SD = 50; and plots without *Lantana*, $\bar{x}$ = 5849 fl., SD = 53). Given the structural invasive nature of *L. camara*, in many natural vegetation plots where it was present, little growth areas was available for NOFPs. Due to the large discrepancy between floral densities, it is difficult to ascertain the influence of *Lantana*'s competitive or facilitative effects on NOFPs flower visitation.

Table 3.3. The effect of *Lantana camara* on NOFPs flower interactions (int.), of different insect flower visitor groups, in natural vegetation, with and without *Lantana*, bordering mango orchards.

Insect Group	**Int. on NOFP flowers with *Lantana* absent**	**Int. on NOFP flowers with *Lantana* present**	**Effect of *Lantana***
Ants	58	4	-54 [93% decrease]
Butterflies	161	28	-133 [82% decrease]
Wasps	18	22	+4
Flies	58	2	-56 [96% decrease]
Bees	21	1	-20
Beetles	9	0	-9

Overall flower visitation (number of interactions) in the mango orchard boundary plots was dominated by bees ($\bar{x}$ = 11, SD = 174) and flies ($\bar{x}$ = 20, SD = 28), whereas ants ($\bar{x}$ = 8, SD = 27), butterflies ($\bar{x}$ = 21, SD = 37) and flies ($\bar{x}$ = 19, SD = 37) dominated flower visitation in natural vegetation (Figure 3.5). The dominant groups visiting mango were flies, bees and ants, most notably *Musca* sp., syrphids (*Eumerus* and *Betassyrphus* spp.), honeybees (*Apis mellifera*) and *Camponotis* sp. *Bidens pilosa* was the only other flowering species encountered in mango orchard boundary plots with a total of 29 observed insect-flower interactions. In natural vegetation plots, *Lantana camara* flowers were predominantly visited by flies, ants, bees, wasps and butterflies. The majority of these flower-visiting species consisted of *Musca* sp., *Pheidole megacephala*, Formicidae sp., honeybee, wild bee sp. (Apidae), and Pierinae sp. (Figure 3.5).

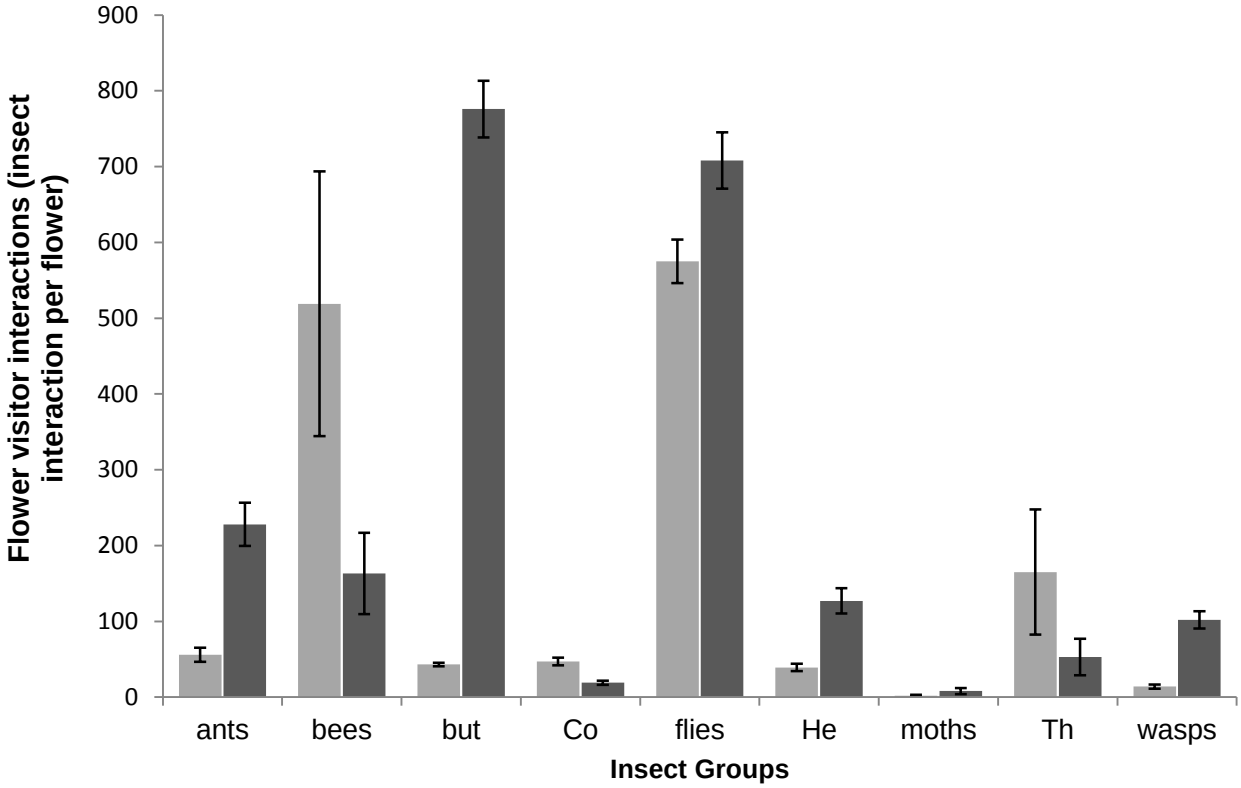

Figure 3.5. Total amount of flower visitation of insect groups in all mango orchard (light grey) and natural vegetation (dark grey) plots observed during June to October 2013. Error bars indicate standard deviation. ants, Hymenoptera (Formicidae); bees, Hymenoptera (Apoidea); but, Lepidoptera (butterflies); Co, Coleoptera; flies, Diptera; He, Hemiptera; moths, Lepidoptera; Th, Thysanoptera; and wasps, Hymenoptera (Apocrita).

Forty seven flower visitor species were shared between mango and other naturally-occurring flowering plants in neighbouring natural vegetation (Table A3, Appendix 1). *Lantana camara* was visited by 43 of these species, specifically species belonging to the Dipteran (11 fly sp.) and Hymenopteran (4 ant, 2 bee and 3 wasp species) groups (Figure 3.6). The most abundantly-shared flower visitors between mango and *Lantana* were honeybees (*Apis mellifera*), native flies (from groups Syrphidae, Tachinidae, Muscidae sp.) and ants (*Camponotis* sp., *Pheidole megacephala* and *Lepisiota sp.*) (Figure 3.6). There were 28 shared insect species that had less than 5 interactions with mango flowers over the entire sampling period, indicating rare/opportunistic visitation events by a diversity of flies (Calliphoridae, other Syrphidae), wild bees (*Ceratina* and *Xylocopa* sp.) and a few butterflies (from the Pieridae, Nymphalidae, Lycanidae and Papilionidae groups) (Figure 3.6).

A total of 1439 flower visitor-mango interactions were observed over the entire mango flowering season, whereas 1722 insect interactions were observed for *Lantana*. In comparing interactions in relation to floral densities, *Lantana* had more interactions with a total floral density of approximately 133 350 flowers to mango, which had a much larger total floral density of about 1 325 000 flowers

(Figure 3.7). The remaining ten other flowering species within the natural vegetation were visited 464 times by 57 species. The flowering species encountered in the natural vegetation plots were *Bidens pilosa*, common daisy (Asteraceae sp.), wild jasmine (*Jasminum multipartitum*), *Justicia flava*, *Ipomoea purpurea*, river heliotropium (*Heliotropium ciliatum*), scotch thistle (*Onopordum acanthium*), syringa (*Melia azedarach*), Milkweed (*Gomphocarpus physocarpus*) and *Tridax procumbens*.

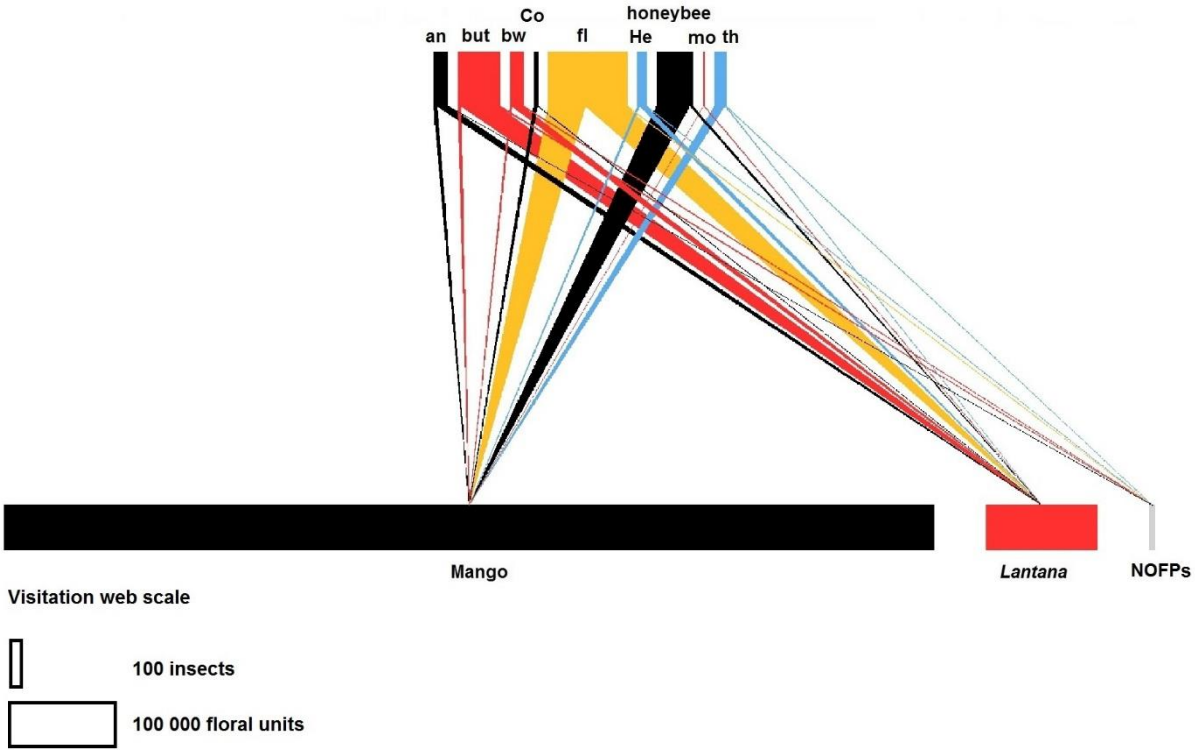

Figure 3.6. Flower visitation web of all pooled data (all interactions observed) from mango orchard boundary and natural vegetation plots surveyed monthly from June to October 2013 in Hoedspruit, South Africa. Flowers of mango, *Lantana* and NOFPs and grouped flower visitors and their abundances are represented by a rectangle with the width of connecting lines indicating visitation frequency. The full species list is provided in Table A3 (Appendix 1). ants, Formicidae, Hymenoptera (black); but, butterflies, Lepidoptera (red); bw, other bees and wasps, Apoidea and Apocrita, Hymenoptera (red); Co, Coleoptera (black); fl, flies, Diptera (yellow); He, Heteroptera (blue); honeybee, *Apis mellifera* (black); mo, moths, Lepidoptera (purple); and th, thrips, Thysanoptera (blue).

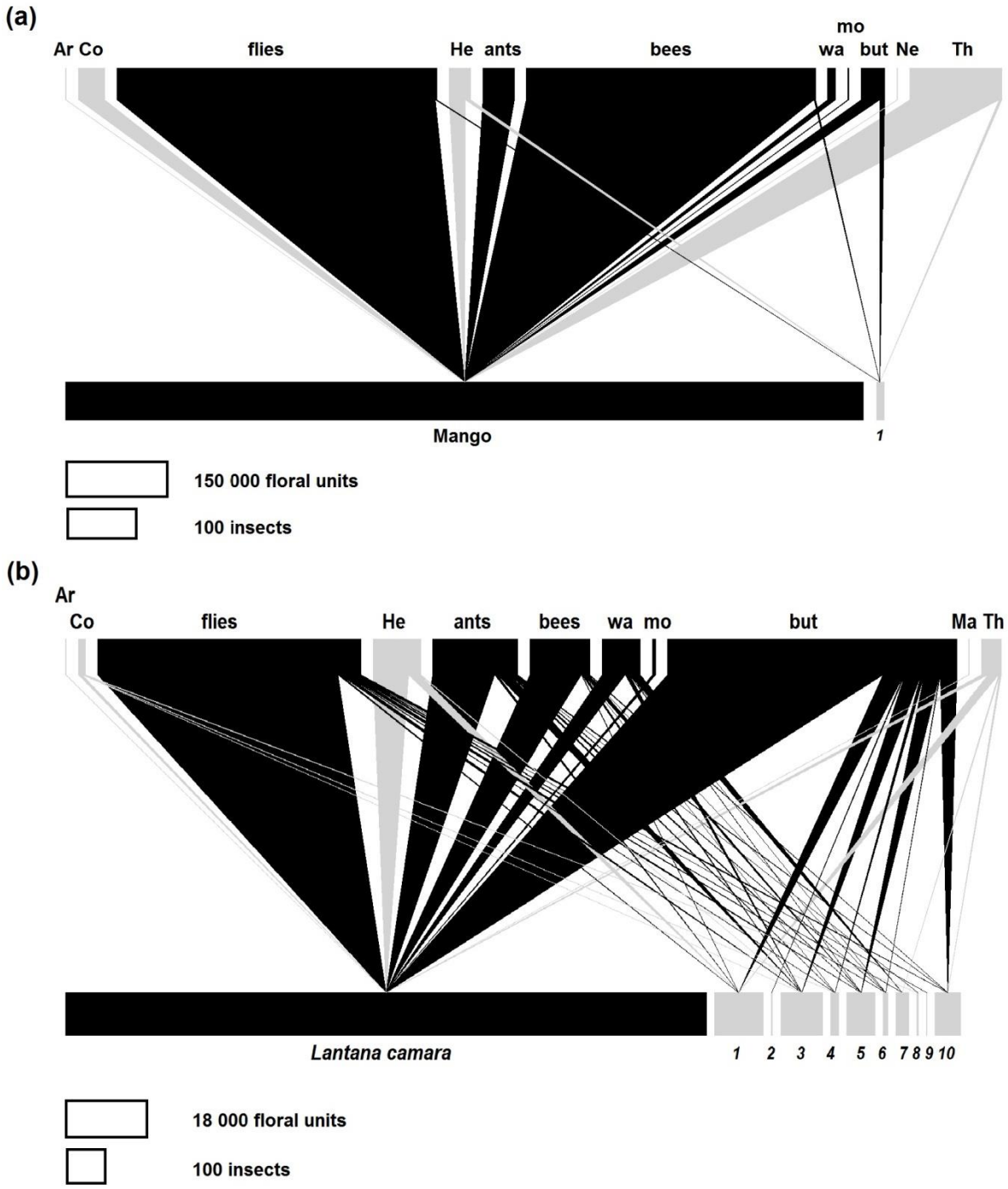

Figure 3.7. Flower visitation webs of pooled data from (a) mango orchard boundary and (b) natural vegetation plots surveyed monthly from June to October 2013 in Hoedspruit, South Africa. Each species of plant and grouped flower visitor and their abundances are represented by a rectangle with the width of connecting lines indicating visitation frequency. The full species list is provided in Table A3 (Appendix 1). Mango, *Lantana* and known mango and *Lantana* flower pollinators are shown in black, other flower visitors and plant species are presented in grey. Ar, Araneae; Co, Coleoptera; flies, Diptera; He, Heteroptera; ants, Formicidae (Hymenoptera); bees, Apoidea (Hymenoptera); wa, wasps, Apocrita (Hymenoptera); mo, moths (Lepidoptera); but, butterflies (Lepidoptera); Ma, Mantodea; and Th, thrips (Thysanoptera).

3.4. DISCUSSION

3.4.1. Flower visitor community composition of mango orchards and bordering natural vegetation

Flower visitor communities in mango orchard boundaries were significantly different to those found in nearby natural vegetation. This could be explained by the differences in key environmental factors governing flower visitor insect community structure (quantity, quality and variety of floral resources present) between mango orchards and natural vegetation (Potts *et al.* 2003). In natural vegetation, the presence of a wider variety of flowering species attracted a greater diversity of flower visitors, such as bees, flies, ants, butterflies and wasps. *Lantana camara* made up the majority of flowering plants in the natural vegetation during mango flowering (winter), as few native plants were flowering in the semi-disturbed areas surrounding mango orchards at this time.

In light of *Lantana*'s attractive flowers and that it is widely abundant in natural vegetation on the fringes of mango orchards, it is no surprise that *Lantana* flower presence increased flower visitor species richness and abundance of the flower visitor assemblages of natural vegetation bordering mango orchards, as well as in nearby mango orchard boundaries (results seen in Chapter 2). Other studies have found IAPs to facilitate native pollinator communities by increasing resource availability, leading to increased flower visitor population sizes, keeping pollinator densities high, extending flight season duration, and increasing the range and promotion of native flower visitor population growth, when flowering before or after the native plant flowering period (i.e. overwintering assistance) (Pyšek *et al.* 2012, see also Graves & Shapiro 2003; Williams *et al.* 2006). However, the shifting nature of IAPs, due to the influences of floral density, spatial and temporal variation, make them undesirable factors in pollination systems as their overall effects on native flora can change from facilitative to competitive (Muñoz & Cavieres 2008).

The high species turnover seen in natural vegetation without *Lantana* is attributed to the unequal lower floral densities of other flowering plants in these natural vegetation plots. Despite low floral densities, natural vegetation is important because it usually provides nesting sites and allows for completion of lifecycles, because of the native plant species present, high levels of natural heterogeneity (i.e. more micro-niches) and low degree of disturbance (Blitzer *et al.* 2012).

Mango orchards, as a mass flowering crop, generally attract large amounts of flower visitors because of the increased resource availability (Hermann *et al.* 2007; Holzschuh *et al.* 2013; Westphal *et al.* 2003). In this case, large amounts of the same species of flower visitors were attracted to mango, namely, honeybees, syrphids and ants (e.g., *Camponotis* sp). Similarly, in a study on flower visitors in restored compared to intensively managed meadows, Albrecht *et al.* (2007) found increased flowering plant species richness correlated with increased insect flower visitor diversity and abundance (see also

Bruckman & Campbell 2014). The composition of flower visitor communities are influenced by variation in floral attractiveness, proximity to nesting localities, habitat heterogeneity and environmental conditions (i.e. climate, sun exposure, and micro-climates) as these factors differ between habitats (Lawton & Price 1979; Potts *et al.* 2003; Price 1984).

It would follow that the flowering species composition influences the composition of the flower visitor community (Potts *et al.* 2003). Comparing insect flower visitors of mango to those of *Lantana camara*, it is apparent that *Lantana* attracts a far larger diversity of insects. This could probably help explain why *Lantana* is such a successful invasive alien plant, i.e., attractive flowers, year-round flowering, strong competitive effects towards native plants and its proliferation in semi-disturbed areas, such as those surrounding mango orchards (Barros *et al.* 2001; Sharma *et al.* 2005). In this case, flies (Dipterans) and wild bees seem to be generalist flower visitors as they visit mango, *Lantana* and other naturally occurring flowering plants in the natural vegetation. Generalists can have a wide floral diet and forage on many flowers occurring in an area (Fontaine *et al.* 2008). As increased flower visitation leads to improved seed-set for *Lantana*, an additional pathway for invasion by *Lantana camara* is created, where it becomes established in an area and eventually naturalizes or out-competes all other native plants and dominates the native flower visitation network (Lopezaraiza-Mikel *et al.* 2007; Memmot & Waser 2002; Pyšek *et al.* 2012; Sharma *et al.* 2005).

The higher visitation rate to *Lantana* can probably be ascribed to its high quality nectar content, which makes it attractive to local flower visitors (average sucrose content = 20 - 28% and 0.39 µL in volume per flower) (Barros *et al.* 2001; Muthoka & Mananze 2005). Whereas mango flowers present a less rewarding nectar quality (average sucrose content = 5% and < 0.1 µL in volume per flower) (DFA 2006). Together with the high nectar sugar content, *Lantana*'s longer (than mangos) corolla tube length attracts a large diversity and abundance of butterflies, however, other flower visitors such as flies, bees, wasps and ants do not seem to be deterred by this functional structure (Barrows 1976; Hamm 2012). Mango's lower quality nectar may make it a less desirable food resource than *Lantana*, as insects have to make more flower visits to mango for the same nectar reward. Nevertheless, mango still received an abundance of flower visitors. This may be because of extra-floral nectaries, discovered by Du Toit & Swart (1993), present at the base of the panicles and panicle branches on mango inflorescences. These additional resources may help to sustain pollinator communities keeping visitation rates constant (Du Toit & Swart 1993).

Caution should be exercised when inferring results reported in this study to other situations as flower visitor assemblages invariably alter due to temporal and spatial changes, be it natural or in response to anthropogenic activity (Petanidou *et al.* 2008). It should also be noted that this is a study on flower visitors which should not be equated to pollinators, as insect flower visitors are able to forage on flowers

without having much effect on pollination, either because their movement does not bring them into contact with pollen or they are unable to carry pollen from one flower to the next (e.g., aphids and thrips). Here, some flower visitor species known to be non-pollinators were included in the visitation networks to provide insight on overall arthropod-flower interactions observed for all species. Some of these visitor species (Araneae, Mantodea and Neuroptera) are known to be predators of pollinating flower visitors and their presence may in fact alter pollinator behaviour, and therefore, flower visitation. As this was not a focus of this study it is difficult to ascertain the scope of these predator's influence on flower visitor behaviour, but acknowledging their presence may provide information to future studies concerning pollinator foraging behaviour.

This case study provides information about the flower visitor community of both sides of farm-natural vegetation margin. It underlines the importance of the conservation of natural areas and patches along and within farmland to facilitate crop pollination. It also highlights how mass flowering crops may influence the continued invasion of invasive alien plants present in bordering vegetation. Investigating pollinator functional diversity in a subtropical area in South Africa, Grass *et al.* (2014) found invasive alien plants and natural habitat loss to detrimentally affect pollinator species richness (of specialists) which would have a knock-on effect for local plant communities, this is particularly problematic in degraded habitats such as the natural areas surrounding mango orchards (see also Biesmeijer *et al.* 2006).

This biodiversity-rich natural vegetation can be of great value to agro-ecosystems by inducing a 'spill-over' effect of flower visitors, also known to be an 'edge effect'. Through this effect there is a higher species diversity of crop flower visitors due to the facilitative benefit from native plants in close proximity, as has also been observed in this system (Blitzer *et al.* 2012; Carvalheiro *et al.* 2010, 2012; Chacoff & Aizen 2006). Crop fields can also contribute to improving pollination services in bordering natural areas, when the 'spill-over' effect occurs in the opposite direction (Blitzer *et al.* 2012). Hanley *et al.* (2011) has shown that bean fields, as mass flowering crops, tend to cause a similar 'spill-over' effect of increased flower visitor species richness and abundance in bordering hedgerows compared to hedgerows bordering wheat fields. Another such study on farmland near forest fragments in Kenya suggest that flower visitor richness in crops has a positive effect on the pollinator community in nearby natural habitat (Hagen & Kraemer 2010). Pollination services on the margins of farmland and natural habitat may in fact overlap as a result of shared flower visitors between crops and native flowering species, contributing to increased native plant fitness in natural habitat (Tuell *et al.* 2008). Within this study, mango and naturally occurring flowering species in natural vegetation shared flower visitors (mainly wild bee, honeybee and fly species, also seen in Chapter 2 results), which is similar to the results of another study done by Carvalheiro *et al.* (2010) in mango orchards in Hoedspruit. Carvalheiro *et al.* (2010) determined that the wild pollinator community, supported by natural areas surrounding

mango orchards, was more important to mango pollination than the additional managed honeybees brought into the orchards during mango flowering. Due to the important biodiversity element that these neighbouring natural areas contribute to services in this pollination system, every effort should be made to ensure healthy functioning through proper management (Garibaldi *et al.* 2014).

Management Recommendations and Future Research

I strongly recommend, along with Carvalheiro *et al.* (2012), that management strategies aimed at boosting wild pollinator population abundances be implemented to further aid in crop pollination. This can be done by conserving small patches of natural vegetation with a variety of local plant species (that flower before and after mango flowering) within mango orchards and, if necessary, plant native plants know to facilitate mango pollination, such as *Aloe greatheadii* and *Barleria obtusa*, in these patches for additional pollination services (Carvalheiro *et al.* 2012; Gurr *et al.* 2003). Implementing constant monitoring of native pollinator populations should be considered as it could act as an early detection method in keeping track of the fluctuations in native pollinator communities. In this way, declines in pollinator communities would be detected immediately and as such a rapid response in crop management could induce facilitative pollination methods to prevent poor crop yields.

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Chapter 4. Thesis synthesis and management recommendations

4.1. The influence of **Lantana** *on mango flower visitors*

In Chapter 2, I set out to determine the effect *Lantana camara* had on mango flower visitation in the flower visitation networks of three commercial mango farms in Hoedspruit. I expected competition to be the predominant effect of *Lantana* on mango. To test this I compared flower visitation to mango where *Lantana* were present with visitation to mango where *Lantana* was absent. *Lantana* seemed to facilitate mango flower visitation as mango plots with *Lantana* had greater flower visitor species richness and abundance compared to those that did not. Along with naturally-occurring flowering plants, *Lantana* seemed to boost mango flower visitation.

In Chapter 3, I investigated the composition of flower visitor communities of mango orchard boundaries and that of bordering natural vegetation. The flower visitor community composition between natural vegetation and mango orchards differed significantly, although they shared a few flower visitor species. In natural vegetation, flies (mostly Syrphids and *Musca* sp.), butterflies, wasps, wild bees and ants played a primary role in the visitation networks, whereas honeybees, wild bees and flies were the main pollinators in mango orchards. Flower visitor communities were significantly different in sites with *Lantana* present, in both mango and natural vegetation. This suggests that the presence of *Lantana* changes the flower visitor community and in this way *Lantana* is intricately involved with mango flower visitor communities in this agro-ecosystem during mango flowering periods.

Having investigated *L. camara*'s influence on mango flower visitation and its involvement in the marginal flower visitation network of a mango related agro-ecosystem, it can be concluded that *Lantana camara* possesses strong attractive qualities in luring a larger abundance and wider diversity of flower visitors, which may provide a facilitative benefit to mango flower visitation and production, as well as altering flower-visiting communities within agricultural flower visitation networks (Chapter 3). Where *Lantana* was present, mango flower visitation by different insect visitor groups were increased for butterflies, flies (by 118%), honeybees (by 144%) and other bees and wasps. Furthermore, it is inferred that *Lantana* benefits likewise by increased flower visitor species abundance and diversity, from the 'magnet effect' created by mango as a mass flowering plant. This effect is expected to have a positive influence on *Lantana*'s reproductive success (through increased seed-set) and so this network provides a susceptible pathway to invasion by alien plants with attractive floral traits.

Despite the increased flower visitor abundance and diversity associated with *Lantana* during mango flowering, I found that *Lantana* does not support mango flower visitors outside of mango flowering periods (Chapter 2). Therefore, it is reasonable to suppose that *Lantana* gains more benefit from the

flower visitation network of mango by co-occurring along orchard boundaries, than any benefit gained by mango from facilitation. This would indicate a beneficial partnership between an alien invasive plant and an insect-pollinated crop. I have shown that *Lantana camara* has integrated into a biodiversity-rich flower visitor community, where it is anticipated to gain reproductive fitness through visitation by generalists occurring in this agro-ecosystem (Chapters 2 and 3). This is consistent with a number of studies (Bartomeus *et al.* 2008; Carvalheiro *et al.* 2008; Olesen *et al.* 2002) which have found that invasive species often integrate into networks via generalist species.

4.2. Should Lantana *be maintained or removed?*

Lantana's multifarious involvement in this agricultural flower visitation network has the potential to make it more troublesome in the future, by making its invasion more difficult to control. As an alien invasive plant it will continue to apply damaging environmental pressures to native plants' reproductive output and ultimately, their survival. *Lantana*, after surpassing the natural area's impact threshold capacity for *Lantana* plant invasion, will continually affect native plant community structure by out-competing natives for resources (such as generalist pollinators) and projecting adverse allelopathic effects (Gooden *et al.* 2009; Vardien *et al.* 2012). Forming thick, impenetrable stands of vegetation, *Lantana*'s proliferation will affect growth of native plants in natural areas (Sharma *et al.* 2005). Grazing potential will also be lost, and so the value of this land will be diminished. It is unknown how this invasional situation will affect the natural vegetation's flower visitor community. Published studies would suggest that a floral community solely dominated by *Lantana* would contain a large proportion of generalist pollinators, being primarily butterflies, flies and wasps, few of which are known to visit mango flowers (Barrows 1976; Hamm 2012; Schemske 1976).

Due to the nature of mango flowering (i.e. mass flowering), relatively few successful pollination events are required to obtain acceptable fruit yields (60 to 70 kgs of fruit per tree) (DAF 2006). Many fruits grow on the trees after mango flowering, with several being removed during pruning (some of these young, green mangoes are used to make mango *atchar*) so that all the tree's resources are directed at developing sizeable fruit to be sold and, if international standards and specifications are met, to be exported. Discussions with farm managers about mango pollination revealed that they are becoming more aware of the value of wild pollinators and that the addition of managed honeybees does not necessarily provide adequate protection against pollination deficit.

Ultimately, the costs incurred to remove *Lantana*, once fully established, through biochemical and physical methods will surpass any slight agricultural profit gained through visitation facilitation and so, given its status as a highly invasive plant, it is recommended that *Lantana camara* be removed from mango orchards (Vardien *et al.* 2012). Particular emphasis should be placed on the importance of the native flower visitor community providing a significant portion of mango pollination services.

4.3. Management recommendations

This study has shown, in some detail, the large proportion of mango flower visitors that are wild (58%) compared to the proportion of managed honeybees (42%). Mango farmers largely rely on a single species (*Apis mellifera*) to ensure their crop's pollination and eventual fruit yield. However, increasing the abundance of this single species will only match its present visitation rates and not replace that of wild flower visitors (pollinators) (Garibaldi *et al.* 2014). This means that the local insect pollinator community is vital to mango farmers. Pollination, in general, is improved with a diverse assemblage of wild pollinators as flower visiting behaviour of every pollinator species is affected differently by insect functional traits, body size, temporal and spatial factors and climatic variables, providing a comprehensive pollinating service (Albrecht *et al.* 2012; Blüthgen & Klein 2011; Hoehn *et al.* 2008; Garibaldi *et al.* 2014).

Garibaldi *et al.* (2014) suggest methods to improve wild pollinator species richness and abundance for sustained crop pollination services. They advocate the addition and maintenance of different food and nesting resources for a diverse assemblage of wild pollinators (providing a range of micro-habitats which incorporate an assortment of substrates known to be used by wild pollinators). Generally, good quality natural areas provide such necessary resources that support wild pollinator communities. As such, it is recommended that patches of natural area within and surrounding mango orchard be conserved or restored and the naturally-occurring floral community within them be maintained. This can be done by planting more native plant species which complement the mango flower visitor community (i.e. wild bees, flies and ants), removing alien invasive plants and restricting the removal or damage of native flowering plants. Carvalheiro *et al.* (2012) used *Aloe greatheadii* (Asphodelaceae) and *Barleria obtusa* (Acanthaceae) to create patches of wild flowers near mango, which resulted in facilitation, benefitting mango flower visitation. Ideally, these natural flowering areas should contain a variety of flowering plants with different phenologies, to sustain pollinators throughout the year, particularly before and after mango flowering. The effectiveness of these patches will likely vary with landscape context, farmland/crop type and floral diversity, abundance and richness (Scheper *et al.* 2013). The use of pesticides, application frequency and timing and the varying, possibly adverse, effects these may have on native pollinators should also be considered as factors affecting flower visitation behaviour and community levels of pollinators (Easton & Goulson 2013; Stokstad 2013)

Programmes focussing on the conservation, preservation and maintenance of natural vegetation areas surrounding mango and patches within orchards should be a priority for crop pollination management. However, these programmes' benefits should also be weighed against implementation and opportunity (in the use of land that can be used for cultivation) costs. This would involve plans focussed on the removal of alien invasive plants within these natural and semi-natural areas. Removal of alien invasive

plants should be done, not only to comply with legislation, but also because the environmental and monetary costs of keeping alien invasive plants far outweigh any benefits offered, be it through flower visitation facilitation or other services.

4.4. Study strengths and limitations

This short term study provides a snapshot view into the current status of *Lantana camara*, as an alien invasive plant, having integrated through flower visitors (as an invasive pathway) into an agricultural flower visitation network. It provides part of ecological baseline data pertaining to how *Lantana camara* is intricately involved in the insect assemblages of natural vegetation and mango orchards boundaries in Hoedpsruit, South Africa. This study may only entail a limited scope of invasional meltdown, but provides sound evidence on which to develop strategies for integrated management of changing landscapes with similar conditions. Case studies, such as the one presented here, are important for understanding invasional pathways and causal effects, along with their potential use in solving problems, such as pollination deficit, experienced within the food production sectors.

As this study only deals with insect flower visitors, an element of uncertainty is maintained on their status as pollinators and pollination efficiency (how many flower visitations lead to successful cross-fertilization). Nevertheless, insect flower visitor species richness and abundance have been shown to be good predictors for pollination success (Carvalheiro *et al.* 2012; Carvalheiro *et al.* 2010; Anderson *et al.* 1982). This short-term study is limited to strictly understanding the effect of an alien plant on mango flower visitation and although closely linked to the pollination process, it might be interesting to know whether successful pollination and increased fruit set are necessarily an outcome of greater visitor abundance associated with *Lantana*.

The effect of the presence of *Lantana* on mango may not extend far into orchards, as different pollinators have different dispersal abilities, so the effect of distance from *Lantana* and mango flower visitation would also need to be assessed. Flower visitation networks are based on direct observational data, but this does not necessarily provide information on species importance and connectedness within these networks. Although every effort was made to maintain constant biotic and abiotic factors within observational plots between surveys, flower visitation patterns will always be affected by spatial and temporal variation (geographic and within-habitat variations) which may result in confounded effects on data which can only be detected through long-term, large scale studies.

4.5. Further research on pollination

Lantana camara, forming a large part of the natural vegetation floral community, increases mango flower visitation but its contribution to mango fruit production is uncertain. Further research should be done on the actual gain in mango production whereby *L. camara*'s facilitation to mango flower visitation increases pollination success, using bagging experiments. Any production value gained should then be compared to similar gains brought about by pollination facilitation by native flowering plant species. Native flowering plants which are able to sustain wild pollinators (important to mango pollination) outside of mango flowering should be identified and their potential supporting role studied. In this way, wild pollinator communities could be maintained year-round, providing a secure and lasting pollination service to mango during flowering season.

This study has indicated that *Lantana* benefits by co-occurring nearby mango. Further investigation into *Lantana*'s seed set by comparing reproductive output of plants in areas with and without mango, would demonstrate whether the observed increase in flower visitor abundance and diversity translates into greater viable seed set for *Lantana*. Given that *Lantana* is known to be self-compatible (i.e. autogamous), it would be interesting to ascertain whether there are differences in seed viability between plants that grow nearby mango and those that do not.

Where there is a deficit in pollination services, priority has to be placed on programmes in agricultural practice investigating methods of increasing (or maintaining) pollination of crops. Here, it has been found that an alien invasive plant contributes to the flower visitation (as part of the pollination service) in and around an agricultural crop. In this situation it is not advisable to preserve dependence on this invasive plant, given the extreme invasive nature of this plant species. Rather, the usefulness of native flowering species, with a great value in sustaining and supporting wild pollinators, should be utilized during evaluation of techniques to restore and increase native pollinator communities. Failure to recognise alternative methods in improving pollination services could be disastrous for the health of natural ecosystems and agricultural systems reliant upon animal pollination.

In the past 20 years, most published literature thoroughly deals with pollination decline in Europe and the USA, but very few studies have been done on pollination service stability in Africa (Aizen *et al.* 2008; Biesmeijer *et al.* 2006; Ghazoul 2005; Johnson 2010; Kennedy *et al.* 2013; Klein *et al.* 2007; Kremen & Ricketts 2000; Le Féon *et al.* 2010; Le Féon *et al.* 2013; Mitchell *et al.* 2009; Potts *et al.* 2010; Van Engelsdorp *et al.* 2012; Vanbergen & IPI 2013; Vanbergen *et al.* 2014). These studies set forth principles to focus on when considering improvement of wild pollinator communities, what works, how it works and why. Unfortunately, these are very Euro-American biased principles with management recommendations that are not always applicable to African, even South African, circumstances. African-based studies would have to be driven by outlined research requirements,

similar to important questions on the conservation of wild pollinators in the UK put forth by Dicks *et al.* (2013). In so doing, we would acquire a better understanding of the wider context in which invasive alien plants integrate into agricultural flower visitation networks and how best to inform farm managers and conservation practitioners on pollination management, such as the biodiversity guidelines set forth by Garibaldi *et al.* (2014).

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Appendix 1

Table A1. Summary details of the farms used in this study

Farm	Honeybee hives	Pesticide application	Mango cultivars in plots
Bavaria	Yes	Yes	Keitt, Tommy Atkinson, Kent, Shelly
Jonkmanspruit	Yes	Yes	Keitt, Tommy Atkinson, Kent, Sensation
Mohlatsi	Yes	Yes	Keitt, Tommy Atkinson, Sensation

Table A2. List of flowering plants recorded throughout the flower visitor surveys in natural vegetation and mango plots (June – October 2013).

Code	Species	Family	Number of flowers
1	*Bidens pilosa**	Asteraceae	680
2	Daisy sp.*	Asteraceae	30
3	*Jasminum multipartitum**	Oleaceae	2882
4	*Justicia flava**	Acanthaceae	734
5	*Ipomoea purpurea**	Convolvulaceae	1447
6	*Heliotropium ciliatum**	Boraginaceae	119
7	*Onopordum acanthium**	Asteraceae	230
8	*Melia azedarach**	Meliaceae	110
9	*Gomphocarpus physocarpus**	Apocynaceae	20
10	*Tridax procumbens**	Asteraceae	525
11	*Lantana camara*	Verbenaceae	± 133 350
12	*Mangifera indica*	Anacardiaceae	± 1 325 000

* Naturally occurring flowering plants (NOFPs)

Table A3. List of flower visitors recorded during June to October 2013 in study plots. Flower visitors were classified to Family (except a few non-pollinators, see Arachnids) and a few have been identified down to species level. Plant/s column identifies which plants insect was observed visiting: 'L' Lantana, 'M' mango, and numbers indicate code of NOFPs from Table A2.

Code	Order	Family	Species	Number of observations	%	Plant/s
1	Arachnid	-		1	0.03	M
2	Arachnid	-		1	0.03	L
3	Coleoptera	Coccinellidae		4	0.11	8
4	Coleoptera	Coccinellidae	*Scymnus* sp.	12	0.33	M
5	Coleoptera	Chrysomelidae		3	0.08	4,M
6	Coleoptera	Chrysomelidae	*Macrocoma* sp.	9	0.25	L,M
7	Coleoptera	Chrysomelidae		2	0.06	M
8	Coleoptera	Chrysomelidae	*Monolepta* sp.	6	0.17	L,M
9	Coleoptera	Chrysomelidae	*Monolepta ursulae*	10	0.28	M
10	Coleoptera	Coccinellidae		1	0.03	L
11	Coleoptera	Coccinellidae		1	0.03	M
12	Coleoptera	Coccinellidae		4	0.11	4,L
13	Coleoptera	Coccinellidae		5	0.14	3,L,M
14	Coleoptera	Coccinellidae		9	0.25	M
15	Diptera	Calliphoridae		1	0.03	M
16	Diptera	Calliphoridae	Blowfly sp.	3	0.08	L,M
17	Diptera	Calliphoridae	Blowfly sp.	2	0.06	M
18	Diptera	Muscidae	*Musca* sp. 1	3	0.08	M
19	Diptera	Muscidae	*Musca* sp. 2	615	16.97	1,3,L,M,10
20	Diptera	Tipulidae	*Nephrotoma* sp.	39	1.08	M
21	Diptera	Muscidae		5	0.14	L
22	Diptera	Tephritidae	Fruit fly sp.	2	0.06	L
23	Diptera	Syrphidae	Hover fly sp.	6	0.17	3,L,M
24	Diptera	Syrphidae	Hover fly sp.	6	0.17	3.L,M
25	Diptera	Syrphidae	Hover fly sp.	3	0.08	L
26	Diptera	Syrphidae	*Eupeodes* sp.	9	0.25	L,5,M
27	Diptera	Culicidae	Mosquitoe sp.	1	0.03	L
28	Diptera	Muscidae	*Musca* sp. *3*	96	2.65	1,3,4,L,5,M,6, 10
29	Diptera	Muscidae	*Musca* sp. *4*	17	0.47	1,3,5,M,10
30	Diptera	Muscidae		8	0.22	1,M
31	Diptera	Muscidae		1	0.03	4
32	Diptera	Muscidae		1	0.03	L
33	Diptera	Muscidae		2	0.06	L,M
34	Diptera	Empididae		1	0.03	L
35	Diptera	Empididae		6	0.17	L,7
36	Diptera	Syrphidae	*Ischiodon* sp.	259	7.14	L,5,M
37	Diptera	Syrphidae		4	0.11	L,M
38	Diptera	Syrphidae	*Betassyrphus* sp.	98	2.70	M
39	Diptera	Syrphidae	*Eumerus* sp.	19	0.52	3,L,M,7
40	Diptera	Syrphidae		3	0.08	M
41	Diptera	Tabanidae	*Tabanid* sp.	8	0.22	L

42	Diptera	Tabanidae	*Tabanid* sp.	40	1.10	3,L,5,M,6,9
43	Diptera	Tachinidae	*Tachinid* sp.	9	0.25	M
44	Diptera	Bombyliidae	*Bombomyia* sp. *1*	14	0.39	L
45	Hemiptera	Aphididae	*Black aphid* sp.	88	2.43	1,L
46	Hemiptera	Reduviidae		21	0.58	L
47	Hemiptera	Cicadellidae	Leafhopper sp.	1	0.03	L
48	Hemiptera	Pyrrhocoridae	Cotton strainer sp.	2	0.06	M
49	Hemiptera	Scutelleridae		5	0.14	3,L,M
50	Hemiptera	Coreidae	Tip wilter sp.	16	0.44	M
51	Hemiptera	Cicadellidae		1	0.03	L
52	Hemiptera	Curculionidae	*Mango seed weevil* sp.	2	0.06	M
53	Hemiptera	Pentatomoidea		1	0.03	M
54	Hemiptera	Reduviidae		6	0.17	L,M
55	Hemiptera	Coreidae		7	0.19	3,L,M
56	Hemiptera	Coreidae		5	0.14	L
57	Hemiptera	Cicadellidae		1	0.03	L
58	Hymenoptera	Formicidae	*Camponotis* sp.	32	0.88	L,5,M,1
59	Hymenoptera	Formicidae	*Combretum* sp.	1	0.03	L
60	Hymenoptera	Formicidae		3	0.08	3
61	Hymenoptera	Formicidae	*Pheidole megacephala*	48	1.32	1,3,L,5,M
62	Hymenoptera	Formicidae	*Polyrhachis gagates*	6	0.17	3,M,10
63	Hymenoptera	Formicidae		5	0.14	L,M
64	Hymenoptera	Formicidae	*Monomorium* sp.*1*	4	0.11	L
65	Hymenoptera	Formicidae		2	0.06	M
66	Hymenoptera	Formicidae	*Lepisiota* sp.	183	5.05	1,3,4,L,5,M,6,10
67	Hymenoptera	Apidae		108	2.98	3,L,5,M
68	Hymenoptera	Apidae	*Apis mellifera*	570	15.72	1,4,L,5,M,6,10
69	Hymenoptera	Apidae		1	0.03	M
70	Hymenoptera	Apidae		2	0.06	M
71	Hymenoptera	Apidae	*Xylocopa caffra*	4	0.11	L
72	Hymenoptera	Vespidae		2	0.06	M
73	Hymenoptera	Braconidae		6	0.17	3
74	Hymenoptera	Apidae	*Ceratina* sp.	9	0.25	L
75	Hymenoptera	Braconidae		7	0.19	L,7
76	Hymenoptera	Vespidae		1	0.03	M
77	Hymenoptera	Vespidae		2	0.06	L
78	Hymenoptera	Chalcididae		22	0.61	3,L,M
79	Hymenoptera	Eucoilidae		4	0.11	L,5,M
80	Hymenoptera	Eucoilidae		2	0.06	L
81	Hymenoptera	Eucoilidae		8	0.22	L,M,7
82	Hymenoptera	Eucoilidae		14	0.39	3,L,M,6
83	Hymenoptera	Braconidae		6	0.17	L
84	Hymenoptera	Braconidae		11	0.30	L,7
85	Hymenoptera	Brachonidae		22	0.61	L,7
86	Lepidopera	Brachodidae		4	0.11	L
87	Lepidopera	Xyloryctidae		4	0.11	L

88	Lepidopera	Gracillariidae	*Spurelina* sp.	2	0.06	M
89	Lepidopera	Noctuidae	*Helicoverpa armigera*	1	0.03	M
90	Lepidopera	Pieridae- Pierinae	*Belenois creona* sp.	81	2.23	1,3,L,5,M,10
91	Lepidopera	Pieridae- Pierinae	*Belenois creona* sp.	1	0.03	L
92	Lepidopera	Pieridae- Coliadinae	*Catopsilia florella*	34	0.94	3,4,L,5,M
93	Lepidopera	Nymphalidae- Danainae	*Danaus chrysippus*	15	0.41	2,4,L,M,10
94	Lepidopera	Nymphalidae- Nymphalinae	*Junonia oenone oenone*	3	0.08	3,L,M
95	Lepidopera	Hespiriinae	*Borbo* sp.	13	0.36	L,10
96	Lepidopera	Pieridae- Pierinae	*Belenois aurota aurota*	64	1.77	1,3,L,M
97	Lepidopera	Hesperiidae- Pyrginae	*Tagiades flesus*	3	0.08	L
98	Lepidopera	Pieridae- Pierinae	*Colotis* sp.	21	0.58	L,5
99	Lepidopera	Pieridae- Pierinae	*Colotis* sp.	17	0.47	1,L,5
100	Lepidopera	Pieridae- Pierinae	*Mylothris agathina*	50	1.38	1,3,L,M,10
101	Lepidopera	Pieridae- Coliadinae	*Eurema hecabe*	66	1.82	1,3,4,L,5,M,10
102	Lepidopera	Lycanidae- Lycaninae	*Anthene definita*	3	0.08	L,M
103	Lepidopera	Pieridae- Pierinae	*Colotis evenina*	44	1.21	1,3,L,M,10
104	Lepidopera	Hesperiinae	*Fresna/Borbo* sp.	26	0.72	L,10
105	Lepidopera	Pieridae- Pierinae	*Colotis subfasciatus*	27	0.74	1,L,5,M,10
106	Lepidopera	Lycanidae- Lycaninae	*Lycaninae* sp.	20	0.55	1,L,5,M
107	Lepidopera	Lycanidae- Lycaninae	*Lycaninae* sp.	1	0.03	M
108	Lepidopera	Pieridae- Pierinae	*Colotis* sp.	147	4.06	1,3,4,L,5,M,10
109	Lepidopera	Pieridae- Pierinae	*Colotis* sp.	10	0.28	1,3,L
110	Lepidopera	Pieridae- Pierinae	*Pieridae* sp.	19	0.52	L,5,M,10
111	Lepidopera	Hesperiidae- Pyrginae	*Pieridae* sp.	7	0.19	L
112	Lepidopera	Pieridae- Pierinae	*Colotis danae* sp.	22	0.61	1,3,L,M,10
113	Lepidopera	Nymphalidae- Heliconiinae	*Hyalites eponina*	14	0.39	3,L,M
114	Lepidopera	Papilioninae	*Papilio demodocus*	2	0.06	M
115	Lepidopera	Pieridae- Pierinae	*Colotis vesta* sp.	87	2.40	1,2,3,4,L,5,6,10
116	Lepidopera	Pieridae- Pierinae	*Pinacopteryx eriphia*	12	0.33	4,L,10
117	Mantodea	Hymenopodinae	*Galinthias amoena*	1	0.03	L
118	Neuroptera	Chrysopidae		1	0.03	M
119	Thysanoptera	Aleolothripidae / Phlaeothripidae		57	1.57	1,L,M,7,10
120	Thysanoptera	Thripidae		156	4.30	M